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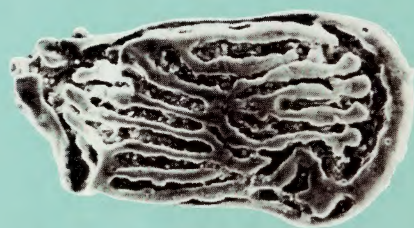

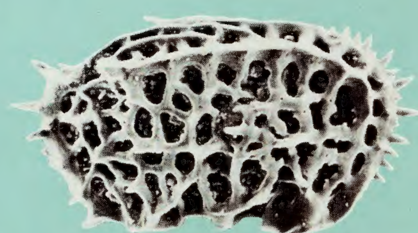

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References should be listed alphabetically at the end of the manuscript. Journal titles must be in full. References to books must give the year of publication, edition, name of publisher and city of publication.

In taxonomic papers synonymies should be of the short form; taxon, author, year, pages, figures. A period and dash must separate taxon and author except in the case of reference to the original description.

Photographs must have clear definition and may be submitted as either glossy or flat prints at the actual size for reproduction. Line drawings for text figures should be in black ink on white card or drawing film. Maximum full-page size is 140 mm wide by 193 mm; single column width is 67 mm. Clear lettering must be inserted. Original drawings up to twice final size are acceptable.

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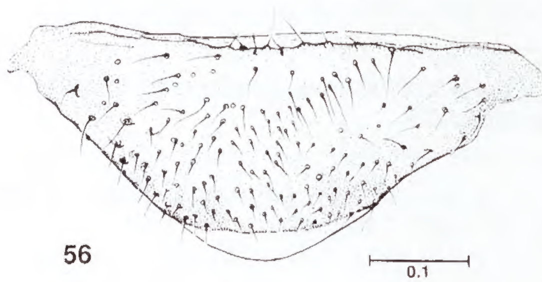
Date of publication

The date of publication of *Memoirs of the Museum of Victoria* volume 53, number 2 was 15 April 1993.

Erratum

Schmidt, E.R. and Thornton, I.W.B. (1993) The Psocoptera (Insecta) of Wilso Promontory National Park, Victoria, Australia. *Memoirs of the Museum of Victoria* 5 137–220.

In the paper by Schmidt and Thornton published in the last issue of the *Memoirs* fi ure 56 (page 158, subgenital plate of *Enderleinella selta* sp. nov.) should be replaced b the figure below. Figure 249 (page 215) of the non-randomised species-individuals di covery curve of psocopterans at Wilsons Promontory 1982–1991 was a repeat of Figu 248. It should be replaced by the second figure below.



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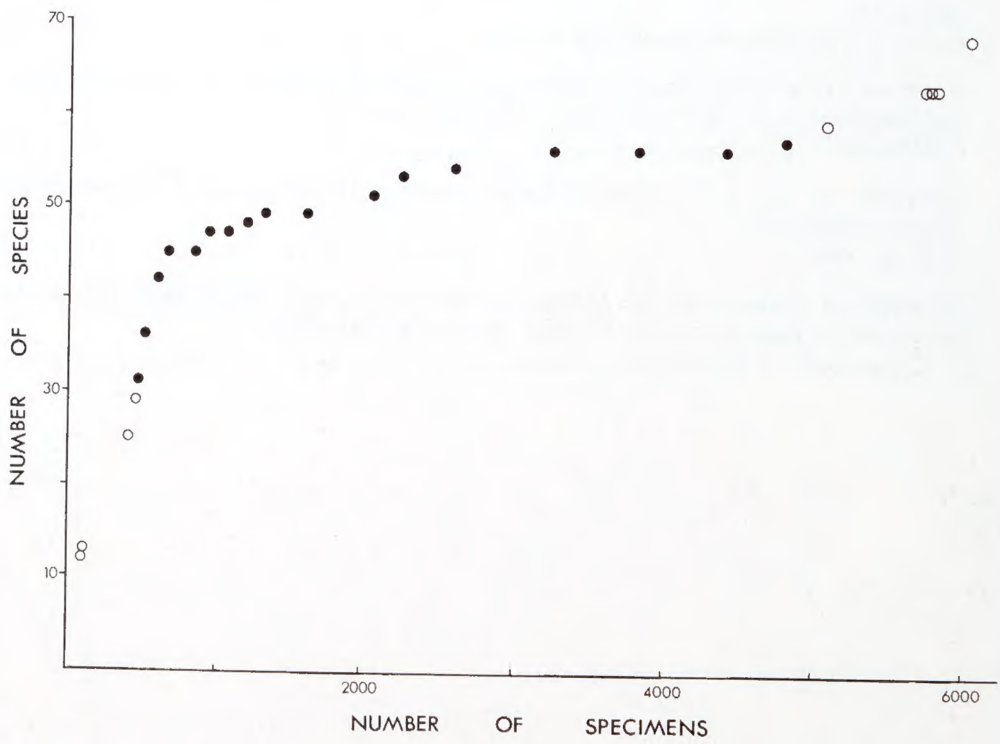

Memoirs of the Museum of Victoria 54: 1–49 (1994)

MIOCENE OSTRACODA OF THE TRACHYLEBERIDIDAE AND HEMICYTHERIDAE FROM THE MUDDY CREEK AREA, SOUTH-WESTERN VICTORIA

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Abstract

Neil, J.V., 1994. Miocene Ostracoda of the Trachyleberididae and Hemicytheridae from the Muddy Creek area, south-western Victoria. *Memoirs of the Museum of Victoria* 54: 1–49.

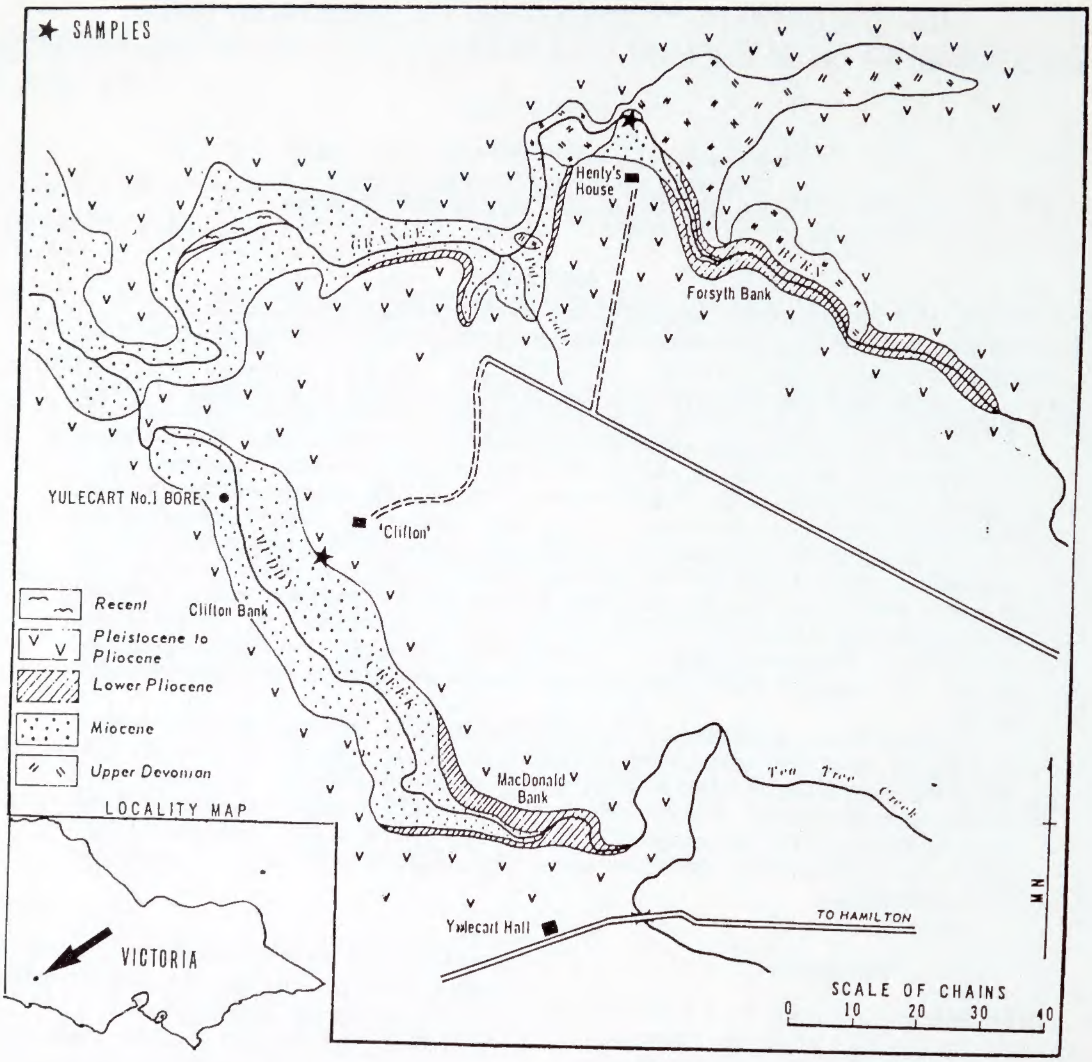
Eleven samples in a vertical section of the Muddy Creek Marl at Clifton Bank, Victoria, Australia, and one large sample from the Marl at Hentys produced nearly 10000 ostracode specimens. The fauna consists of 186 species from 85 genera. Of the Trachyleberididae and Hemicytheridae, 36 species are present. Of these, 15 species are new: *?Alatahermanites septarca, Deltaleberis warnei, 'Hemicythere' lubrica, 'H'. tenuicostata, Mackenzina foveolata, Notocarinovalva yulecartensis, 'Hermanites' thomasi, H. glyphica, Spinobradleya nodosa, Bradleya (Quasibradleya) pyxos, Quadracythere (Hornibrookellina) hentyensis, ?Dumontina cratis, Arculacythereis tatei* and *'Ambostracon' recta.* Three species are left in open nomenclature. Two previously described species have been reassigned: *'Cytheralison' postdeclivis* (Chapman, 1914) to *?Arculacythereis* and *Cythere flexicostata* (Chapman, 1914) to *Chapmanella* gen. nov. Three new genera and one new subgenus have been erected: *Chapmanella, Mackenzina, Notocarinovalva* and *Quadracythere (Hornibrookellina).*

The faunas have a warm-temperate to subtropical character, and indicate a shallow-water, high-energy, near-shore environment of deposition, with abundant phytal associates. The age of the samples ranges from late Early to early Middle Miocene (N8–N10); that is, from late Batesfordian, through the Balcombian to early Bairnsdalian stage, on the basis of planktonic foraminifers. The deposition of the beds in the section at Clifton Bank has occupied a period of approximately one million years. The sample from Hentys is a long-ranging thanatacoenosis.

Introduction

The ostracode fauna of the Muddy Creek Marl in south-western Victoria, Australia (Text-fig. 1) has been described by Neil (1992). Eleven samples from Clifton Bank on Muddy Creek, and one large sample form Hentys on Grange Burn, provided nearly 10000 specimens. The fauna consists of 186 species from 85 genera. Within this fauna, 37 species are new, five new genera will be erected and 57 species have been left in open nomenclature. More than 40% of the specimens, 36 species from 23 genera and 4 subgenera, are members of Trachyleberididae and Hemicytheridae. Three genera, one subgenus, and 14 species are described as new. Four species are left in open nomenclature. This preponderance of trachyleberids and hemicytherids is markedly different from the Miocene fauna from Fossil Beach, Mornington, Victoria which was monographed by Whatley and Downing (1983). The fauna had only 8.2% of individuals (as distinct from separate specimens) from the Trachyleberididae and Hemicytheridae — in all, five species, of which only one, *Bradleya [Bradleya] praemackenziei*, is a hemicytherid.

The dominant species (10% or more of the specimens) in the assemblages from the Clifton Bank samples were *Quadracythere (Q.) spica, 'Hermanites' thomasi* and *Hermanites glyphica. 'Hermanites' thomasi*, endemic to Clifton Bank, constituted more than 30% of the specimens in one of these samples, whereas Whatley and Downing (1983) found that *Bradleya (B.) praemackenziei*, the most abundant of the five species of hemicytherids and trachyleberids referred to above, constituted only 7% of the total. The Hentys sample had no dominant species as defined above, but the commonest (>100 specimens) were *Quadracythere (Q.) spica, Quadracythere (Hornibrookellina) hentyensis, Hermanites glyphica* and *Chapmanella flexicostata.* Of these species *Q. (Hornibrookellina) hentyensis* is endemic to Hentys. By percentage, hemicytherids were dominant at both localities — 34.7% compared to 5.4% for trachyleberids,



Text-figure 1. Clifton Bank and 'Hentys' localities, Yulecart, near Hamilton, southwestern Victoria.

though the latter group were more common at Hentys (8.2%) than at Clifton Bank (3.3%).

The figured specimens (numbers prefixed NMV P) are housed in the Invertebrate Palaeontology Collections of the Museum of Victoria. Faunal slides from the samples used in the preparation of this study are in the collection of the author.

Provenance of the fossils

To the west of Hamilton, the Wannon River has been diverted along the margin of the Newer Basalt which forms much of the plains of the Western District. Several tributaries, notably the Grange Burn and its tributaries Muddy Creek and Violet Creek, have cut through the basalt capping, exposing sediments of Miocene and Pliocene age (Text-fig. 2). These sediments, shallow marine further west, but grading or intergrading into terrestrial deposits in the eastern section nearer to Hamilton, are richly fossiliferous.

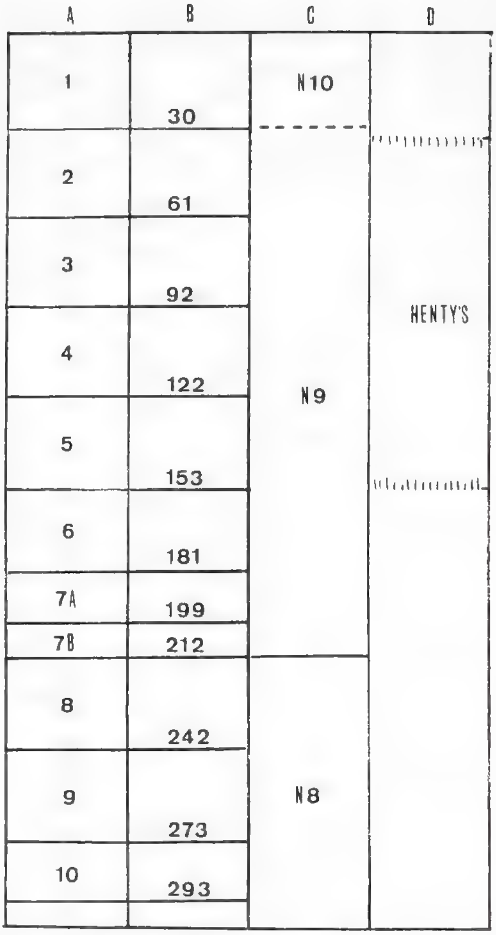
The basement is mid-Palaeozoic rhyolite, on which thin shelf deposits have been laid down. The oldest of these is a limestone, in part crystalline and described by Mallett (1977) as a coarse, yellow-brown calcarenite. Overlying the calcarenite is an unlithified calcareous silty sand, generally green-grey in colour, but tending to fawn or brown in the Grange Burn outcrops as depth of deposition increased and glauconitic effects gave way to ferruginous ones. The presence of coarser lag deposits throughout this sequence is notable, particularly in the upper section (Reeckmann, 1974). The base of the overlying coquinas is defined by a phosphatic nodule bed which marks a discontinuity between the 'marls' and the 'coquinas' (Gill, 1957; Carter, 1978). The lithologies in both the Grange Burn and Muddy Creek exposures show considerable lateral variation. In places, the coquinas give way to shelly silts, grading upward into laminated and sparsely fossiliferous silts which include a tuffaceous band. The final marine deposits at the top of the sequence are represented by a coarse green calcarenite up to 4 m thick. Terrestrial and lacustrine deposits cap the sequences immediately below the basalt, and in places a soil profile is developed in the top of the terrestrial beds (Gill, 1957) which are fine white siliceous sands.

Trachyleberididae and Hemicytheridae

There is partial agreement between the proponents of classificatory schemes for the Trachyleberididae and Hemicytheridae (Neale, 1959; Howe, Sylvester-Bradley, van den Bold and Reyment, 1961; van Morkhoven, 1962; Pokorny, 1955, 1957, 1964; Hazel, 1967; Benson, 1972; Hartmann and Puri, 1974; Liebau, 1975, McKenzie and Bonaduce, 1991). Pokorny's analysis suggested that whatever features are used to diagnose these families, a horizontal, polyphyletic classification will result. In practical terms, progress has been made towards establishing some features as primitive and others as advanced. The Hemicytheridae are generally agreed to be derived from Trachyleberididae. The features about which there is the greatest agreement are the single v-shaped or hooked frontal scar for the trachyleberids and the divided frontal scar for the hemicytherids, together with the six-jointed antennula for most trachyleberids compared to the five-jointed one for hemicytherids (McKenzie and Bonaduce, 1991), and the presence of complex chitin supports in the thoracic limbs of hemicytherids versus simple chitin supports in the legs of trachyleberidids. Other features such as subcentral tubercles, spines, marginal denticulations and eye-spots can be taken as part of a constellation of characters to determine family-level classification but singly they cannot be used safely for diagnostic purposes above genus. For the palaeontologist, soft-part differentiation cannot be applied.

The classification of Hartmann and Puri (1974) is generally followed here. They allowed some trachyleberids exceptionally to have 2 or 3 frontal scars and refused to rule out the possibility of some hemicytherids having v-shaped frontal scars, although none is yet known. The basic reason for this equivocation is the widely accepted transitional nature (in terms of carapace morphology) of many genera. The erection of 'form genera' on the basis of these morphological differences may or may not be consistent with the phylogeny of the species and genera so defined.

Hartmann and Puri endeavoured to strike a balance between neontological and palaeontological principles but Pokorny's original warning remains. The taxonomist faced with the practical problems of developing a phylogenetic classification to cover both neontological and palaeontological taxa must be subjective in weighting characters. The acceptance of weighting is part of the legacy of adopting a conservative taxonomy. In the approach adopted here, the frontal scar characteristics are taken as diagnostic for fossil trachyleberids and hemicytherids. If a cladistic approach were adopted shared–derived features such as muscle scars and frontal scars would be looked for and morphoclines, with or without polarity, would be established to eliminate poly-



Text-figure 2. Clifton Bank and 'Hentys' sections on Muddy Creek and Grange Burn. A, Clifton Bank sample numbers. B, depth from surface in centimetres. C, planktonic foraminiferal zones (Berggren, Kent and Flynn, 1985). D, 'Hentys' sample (time averaged).

phyletic and paraphyletic genera. Pokorny's criticism of a horizontal classification would be tackled at its source.

Liebau (1975: 373) wrote: "New suprageneric taxa should correspond to new information about natural relationships. The production of tribes and subfamilies within the taxonomy of the Trachyleberididae s.l. does not always correspond to an adequate increase of knowledge about evolution, nor to the development of a more practical system either, but is mainly the result of 'taxonomic accidents' (subjective synonyms, caused by uncorrelated taxonomic studies; nebulous phylogenetic ideas, neglecting the main part of observable data; old-fashioned form group concepts and general lack of adequate taxonomic standards)". Hartmann and Puri (1974) advised keeping the number of systematic units in the Trachyleberididae and Hemicytheridae to a minimum. They retained the Thaerocytherinae as a subfamily within the Hemicytheridae, consonant with Liebau's idea, and I concur with their decision.

Trachyleberididae Sylvester-Bradley, 1948

Trachyleberidinae Sylvester-Bradley, 1948 s. s.

Tribe **Trachyleberidini** Sylvester-Bradley, 1948

Trachyleberis Brady, 1898

?*Trachyleberis robustus* (Yassini and Jones) comb. nov.

Pl. 1 figs 1, 2, 3; pl. 14 fig. 1

Actinocythereis robustus Yassini and Jones, 1987: 823, figs 4.1, 4.2.

Figured specimens. NMV P123216 — Pl. 1 fig 1, Pl. 14 fig 1; NMV P134937 — Pl. 1 fig. 2; NMV P134938 — Pl. 1 fig. 3.

Dimensions. (P123216) RV: L=0.92; H=0.50.

Material 23 specimens, Clifton Bank and Hentys, Muddy Creek Marl, early Middle Miocene.

Remarks. The muscle scar pattern, with two frontal scars, a hooked dorsal adductor and a divided ventromedian adductor, is quite distinctive for a trachyleberid (Pl. 14 fig. 1). The two frontal scars are an unusual variant in Trachyleberidinae (Hartmann and Puri, 1974; Hazel, 1967). There is a very large, broad-ended spine developed at the posteroventral angle, and the spines coalesce to form a ventral ridge, extending from the anterior margin to short of the large spine at the posteroventral angle.

Although the development and size of the tubercles/spines is greater in these specimens than in the specimen of *Actinocythereis robustus* figured by Yassini and Jones (1987), their placement and orientation is such that these specimens may be conspecific. However, the assignment of this species to *Actinocythereis* cannot be sustained since there is no linearity in the arrangement of the tubercles/spines, the major diagnostic feature of that genus (Moore, 1961: Q334; Von Morkhoven, 1963: 178). Assignment to *Echinocythereis* on the basis of the double frontal scar is ruled out because *?Trachyleberis robustus* has stout tubercles/spines, randomly

distributed, unlike *Echinocythereis*, in which the spines are finer and the arrangement tends to concentric lines.

I assign the species tentatively to *Trachyleberis* on the basis of its tubercles/spines. Though this is a limited basis, Brady's (1898) diagnosis of the genus refers only to the tubercles/spines of the hard parts, the remainder of the diagnosis being entirely concerned with the soft parts. The assignment is tentative because of the unusual muscle scar and frontal scar pattern, and the quadrate valves. This latter characteristic is shared with *Ponticocythereis* McKenzie, 1967 but *?T. robustus* has well-developed spines all over the valve surface. On the other hand, *T. tridens* Hornibrook, 1953 does show a very similar pattern of tubercles/spines and has a subquadrate shape like *?T. robustus*. The former species has single frontal scar and no anterocentral tubercle like *?T. robustus.* Yassini and Jones (1987) did not refer to muscle scars in their description of *?T. robustus.*

?Trachyleberis robustus occurs at both localities and is distributed among the samples similarly to *?Actinocythereis* sp. A. With more material, it is possible that conspecificity will be confirmed but assignment to *Trachyleberis* s.s. will not be so resolved since the frontal scar is double and the adductors are unusual. *?Trachyleberis robustus* is another species from this fauna which appears to range from the Miocene to the Recent.

Actinocythereis Puri, 1953 (as diagnosed by Hazel, 1967)

? ***Actinocythereis*** sp. A

Pl. 1 figs 4, 5

Figured specimens. NMV P123221 — Pl. 1 fig. 4; NMV P134939 — Pl. 1 fig. 5.
Dimensions. (P123221) LV: L=0.80; H=0.42.
Material. 39 specimens, Clifton Bank and Hentys, near Hamilton, Muddy Creek Marl, early Middle Miocene.

Remarks. Actinocythereis is chosen tentatively for this species because of the linear arrangement of spines. Marginal spinosity is marked. A v-shaped frontal scar is indistinct in one specimen but the adductors cannot be seen because of the co-incidence of two large spines with the muscle scar node. There is minor resemblance to the type species *A. exanthemata* (Ulrich and Bassler) in type of ornament but insufficient characters can be identified to attribute the species unequivocally to this genus or to establish specific identity.

The material exhibits some distinctive characters. The eye tubercle is strong and prominent and in some specimens reddish in colour. In the anterior section, the spines are in four, rather than three, lines. The subcentral tubercle has two prominent spines, and the marginal spine at the posterodorsal angle is terminally trifid. The spines on the lateral surface of the valve terminate with a pore opening.

Ponticocythereis McKenzie, 1967

Remarks. This genus, by original diagnosis, differs inter alia from *Trachyleberis*, which has a subacuminate posterior, in its subquadrate shape in lateral view. The species described hereunder is tentatively placed in *Ponticocythereis* using lateral valve shape as a fundamental diagnostic feature. McKenzie (1967) remarked that for *Ponticocythereis* the "pattern of surface ornament (which is consistent in all known species) suffices to distinguish it from *Trachyleberis* which is spiny over the entire surface". This distinguishing characteristic, regarded as less fundamental than valve shape by Whatley and Titterton (1981), is lost in the present case, where the "'scale'-like protuberances" (to use their terminology) substantially cover the lateral surface of the valves.

?***Ponticocythereis*** sp. aff. *P. manis* Whatley and Titterton, 1981

Pl. 2 figs 3, 4, 5

Trachyleberis sp. 2. — Scott, 1974: 125, pl. 9 figs 97-98.

Figured specimens. NMV P134945 — Pl. 2 fig. 3; NMV P134946 — Pl. 2 fig. 4; NMV P123217 — Pl. 2 fig. 5.
Dimensions. (P123217) RV: L=0.74; H=0.36
Material. 25 specimens, Clifton Bank (rare) and Hentys, Muddy Creek Marl, early Middle Miocene.

Brief description. Very spinose, subquadrate species of *?Ponticocythereis.* Squamose spines have a flattened and somewhat 'daisy'-shaped top (Pl. 11 fig 2), giving the appearance of having been squashed in a direction normal to valve surface (cf. *Trachyleberis* sp. 2. [Scott, 1974 unpublished]). 'Scales' cover valve surface including dorsum and venter, except for furrows parallel and close to anterior and posterior margins and 2 small central areas. Hinge strongly holamphidont. Muscle scars, with clearly v-shaped frontal scar, of characteristic trachyleberid form. RPCs are numerous.

Remarks. This species is very similar to *Ponticocythereis manis* Whatley and Titterton, 1981,

from which it differs in lacking the more spinose marginal denticulation and in having only a small, inconspicuous eye tubercle. The 'scales' show no concentration into a median ridge, as in Whatley and Titterton's species, nor is their surface punctate. The valves of *?P.* sp. aff. *P. manis* are more quadrate than of the other species which has an anterior hinge ear. There is considerable intraspecific variation in the form and distribution of the spines. Some specimens have a few squamose spines around the margins of the valve, with the remainder of the spines being more rounded at the ends. Other specimens have openings or 'pores' in the flattened 'scales'.

This species differs from *P. militaris* (Brady, 1866), *P. icthyoderma* (Brady, 1890) and *P. spinosa* Whatley and Titterton, 1981, all of which have large, often backward-directed spines with a linear arrangement, in the nature and distribution of its spines. Sylvester–Bradley and Benson (1971) referred to the spines of *Ponticocythereis militaris* as 'clavae', where the terminal extension of the spine is longitudinal to the orientation of the valve, but the flattened 'scales' of *?Ponticocythereis* sp. aff. *P. manis* are not clavae. The hinge structure shows the anti-slip bar of *P. manis* s.s. The quadrate shape of the valves and the unusual form of the spines are sufficiently distinctive from *Ponticocythereis* s.s. to suggest that a new genus, inclusive of *P. manis* and *?P.* sp. aff. *P. manis,* might be considered.

Cletocythereis Swain, 1963

Discussion. The genus had a confusing beginning, with Swain using *Cythere rastromarginata* Brady, 1880 as the type species, but not redescribing or refiguring it. Swain assigned a new species, *C. noblissimus,* to the new genus, describing and figuring it in detail, and the diagnosis of *Cletocythereis* reflected this latter species rather than the type species. Since *C. noblissimus* is not congeneric with *C. rastromarginata* (McKenzie, 1967: 232) and has been assigned to *?Acanthocythereis* by Hazel (1967) the genus needs rediagnosis. Benson (1972) published figures of *C. rastromarginata*, established a lectotype, and referred to the problem. The generic concept of *Cletocythereis* is now much more firmly based and Malz (1980) discussed it in detail, and erected new species and subspecies.

The presumed derivation of *Cletocythereis* from *Hermanites* (Holden, 1967, 1976) was based on an assumption that Pliocene/Pleistocene occurrences were the earliest appearances of the genus. However, confirmed occurrences from the Eocene and Oligocene (McKenzie, 1979; McKenzie et al., 1991) and Miocene of Australia (Whatley and Downing, 1983; M. T. Warne, 1987 — pers. comm. and this paper) and unconfirmed ones from the Maastrichtian of Jamaica (Hazel in Benson, 1972) rule out *Hermanites tschoppi* (*H. paijenborchiana* auctt.) as the ancestor. Benson (1972) suggested that *Cletocythereis* could be antecedent to *Hermanites*, and this is supported by its occurrence in the Late Eocene of Australia (McKenzie, 1979). It is clear that identification of derived characters as a preliminary to drawing phylogenetic inferences can be rather subjective when the stratigraphic ranges of species have not yet been investigated fully. Even the v-shaped frontal scar, generally accepted as a relatively primitive feature, is not a safe guide in the case of *Cletocythereis.* Benson (1972) referred to "a partially divided v-shaped frontal scar", and consequently placed *Cletocythereis* early in the line of development from ancestral trachyleberids. Yet within the populations of Miocene *Cletocythereis* species described hereunder, intraspecific variations in the shape and divisions of the frontal scar or scars are considerable — ranging from a single v-shaped scar, through partially divided scars and two scars, one of which is v- or heart-shaped, to two or three more or less circular scars. Of these variations, however, the single v-shaped frontal scar is by far the most common.

In spite of the necessity for caution, I concur with Hartmann and Puri's placement (1974) of *Cletocythereis* in Trachyleberididae, because the v-shaped frontal scar is the most common. The classification of Liebau (1975), which puts not only *Cletocythereis,* but also such genera as *Oertliella* and *Agrenocythere* into Hemicytheridae cannot be supported using the conservative muscle-scar criterion.

Cletocythereis caudispinosa (Chapman and Crespin, 1928)

Pl. 1 figs 6, 7, 8, 9

Cythere caudispinosa Chapman and Crespin *in* Chapman et al., 1928: 125, pl. 9 figs 64a, b .— McKenzie, 1974: 160, pl. 1 fig. 4.

Oertliella caudispinosa. — McKenzie, 1981: 107.

'Oertliella' caudispinosa. — McKenzie and Peypouquet, 1984 : 293.

Cletocythereis caudispinosa. — Whatley and Downing, 1983: 382, pl. 7 figs 10, 11. — Warne, 1987: 442.

Cletocythereis cf. *caudispinosa.* — McKenzie et al., 1991: 172, pl. 8 fig. 14, pl. 9 fig. 6.

Figured specimens. NMV P134939 — Pl. 1 fig. 6; NMV P134940 — Pl. 1 fig. 7; NMV P134941 — Pl. 1 fig. 8; NMV P123327 — Pl. 1 fig. 9.
Dimensions. (P123327) LV L=0.67; H=0.39.
Material. 65 specimens from Clifton Bank and Hentys, near Hamilton. *C. caudispinosa* also occurs in the Wuk Wuk Marl at Bairnsdale in Gippsland; in the lower section of the Morgan Limestone at Blanchetown, SA; and in the Mannum Formation at the Mannum Pumping Station, SA. A related and possibly ancestral form occurs in the Tortachilla Limestone and the Blanche Point Marls of the Port Willunga area of SA (personal collections) and was noted by McKenzie et al. (1991).
Horizon and Age. Muddy Creek Marl, early Middle Miocene. If the specimens from the Wuk Wuk Marl and the Morgan Limestone are conspecific, they are also contemporaneous (Abele *in* Douglas and Ferguson, 1988; Lindsay, 1985).

Description. There is a distinct eye tubercle. Halfway along the dorsal margin a 'rim tooth' (McKenzie, 1974) or 'aussenzahn' (Malz, 1980) projects above the general line of the LV and in dorsal view overlaps the RV. Hinge strongly holamphidont with smooth simple teeth and a smooth median bar. Anterior margin finely denticulate and fused zone broader than at other parts of the margin. Approximately 20 simple, unbranched radial pore canals. Anterior marginal ridge thin, sharply defined and stands up normal to lateral surface of the valve. Ventral ridge continuous with anterior ridge, thin and also sharply defined, at least in specimens from Muddy Creek. Dorsal ridge less clearly defined than for *C. rastromarginata* (Brady, 1880) but a series of 3 well-developed subacuminate nodes gives a broken dorsal profile in lateral view.

Posterodorsal angle marked by development of a short spine, as remarked by Chapman et al. Muscle scars consist of 4 adductors in a near-vertical row, each scar obliquely aligned to the ventral margin. Dorsal and ventral scars short and rounded, the middle two scars are elongate and somewhat dumbbell-shaped. Frontal scars vary, but the commonest form is a small, circular scar, with a larger v- or heart-shaped scar below it in lateral view. In some specimens the larger frontal scar has the apex of the v pointing anteriorly, rather than ventrally. In juvenile forms, the larger frontal scar is more attenuated in shape, and the smaller dorsal scar may be absent.

Remarks. Chapman and Crespin's description of the holotype is not detailed. Unlike the type species, *Cletocythereis rastromarginata* (Brady, 1880), for which Benson (1972) illustrated and designated a lectotype, *C. caudispinosa* has not been redescribed.

Chapman and Crespin's description emphasised the acuminate spinose posterior, anterior and ventral ridges, and reticulation pattern. Although they stated that 'the aureole of the median area is not distinctly radiate', in some specimens the reticulation around the subcentral tubercle is very regularly developed, except directly ventral to the tubercle. In the figured specimen, the reticulation is marked by substantial 'celation' (Sylvester–Bradley and Benson, 1971) or intergrowths which tend to obscure the pattern (Pl. 11 fig. 1).

A possibly ancestral form from Eocene beds in South Australia differs from the Muddy Creek specimens in that the dorsal ridge has spines rather than nodes, the ventral ridge is not continuous with the anterior ridge, and the posterior spines are less well-developed. However, the acuminate posterior and reticulation strongly suggest *C. caudispinosa* rather than *C. rastromarginata*. Muscle scars were not observed in these specimens so a possible relationship with the genus *Oertliella* cannot be established, even though other morphological features such as the spinose dorsum suggest it.

Cletocythereis sp. cf. *C. rastromarginata* (Brady, 1880)

Pl. 1 fig. 10, Pl. 2 figs 1, 2

Cythere rastromarginata Brady, 1880 (partim, sensu Holden, 1967): 83, pl. 16 figs 1a–d (not figs 2a–d = *C. bradyi* Holden, 1967). — Puri and Hulings, 1976: 286, pl. 9 figs 10–14 [not 9 = *C. bradyi* Holden, 1967].

Bradleya rastromarginata. — Hornibrook, 1952: 17.

Cletocythereis rastromarginata. — Swain, 1963: 823. — Benson, 1972: 22–23, 28, 56, pl. 1 figs 1–4. — Hartmann, 1981: 108, pl. 5 figs 15, 16. — Yassini and Wright, 1988: 169, figs 6 – McKenzie et al., 1990: 20–21, pl. 6 fig. 9, pl. 8 figs 11, 12.

Cletocythereis cf. *rastromarginata*. — McKenzie, 1967: 95, pl. 13 figs 1–2, fig. 6b, figs 10a–b. — Hartmann, 1978: 96, pl. 6 fig. 16. — Hartmann, 1979: 234, pl. 6 figs 5–7. — Malz, 1980: 382. — Warne, 1987: 442. — McKenzie et al., 1991: 171, pl. 8 fig. 13, pl. 9 fig. 2.

Cletocythereis sp. — McKenzie, 1979: 91, pl. 2 figs 4, 5.

Figured specimens. NMV P134942 — Pl. 1 fig. 10; NMV P134943 — Pl. 2 fig. 1; NMV P134944 — Pl. 2 fig. 2.
Dimensions. (P134942) Male LV L=0.77; H=0.36.
Material. 48 specimens from Clifton Bank and Hentys, near Hamilton, Muddy Creek Marl, early Middle Miocene.

Brief description. Elongate species of *Cletocythereis* with finely denticulate anterior and strongly denticulate posteroventral margin. Dorsal margin straight. Posterodorsal margin concave. Ventral margin slightly concave. Fine-ribbed reticulation, tending to concentric about

the subcentral tubercle. Strong ventral marginal rib.

Remarks. These specimens differ from the lectotypes figured by Puri and Hulings (1976) in being much less inflated and in lacking the nodes on the ventral ridge. Holden's (1967) resolution of the problem of alate and non-alate forms of *C. rastromarginata* (Brady) by treating them as separate species is correct (Malz, 1980). Since the specimens from Clifton Bank and Hentys are non-alate forms, they are referred to *C. rastromarginata.* Some variation occurs in the form of the anterior ridge but this is also evident from the figures in Benson (1972). Sexual dimorphism in terms of length/height ratios confirms Holden's division of Brady's original specimens into two species. Benson (1972) did not include an amended diagnosis to replace Swain's original description (1963) and, unfortunately, the material available to me is insufficient in quantity and quality to enable an amended diagnosis to be included.

Tribe **Veeniini** Puri, 1973

Dumontina Deroo, 1966

Discussion. This genus is not represented by any other described or figured species from Australian fossil or Recent faunas, except for one species listed by Warne (1987). However, hingement and *Cythereis*-like shape, with the trachyleberid muscle scar of ?*Dumontina cratis* sp. nov. suggest this genus. Erection of a new genus for this species and ?*Dumontina* sp. A may be warranted after further study.

?*Dumontina cratis* sp. nov.

Pl. 2 figs 6, 7, 8

Holotype. NMV P123218 — Hentys — Pl. 2 fig. 8.
Paratypes. NMV P123219 (not figured); NMV P134947 — Pl. 2 fig. 6; NMV P134948 — Pl. 2 fig. 7.
Dimensions. Holotype LV: L=0.73; H=0.38. Paratype (P123219) RV: L=0.64; H=0.35.
Material. 57 specimens, Clifton Bank (older samples only — 7 to 10) and Hentys, Muddy Creek Marl, early Middle Miocene.

Diagnosis. Robust *Dumontina*-like species with strongly developed, finely-meshed reticulation and deep sulci in anterior and posterior.

Description. Valves strongly calcified and thick; dorsal and ventral margins straight; valve tapered posteriorly; anterior smoothly and broadly rounded; posterior rounded with slight angularity at extremity. Strong, stub-like denticulations on full anterior and posterior margins (where not broken or worn); denticulations continued along anteroventral and posteroventral margins. Thick marginal anterior and posterior marginal ribs, covered with nodules; these ribs separated from reticulated lateral surface of valves by deep sulci, with nodules protruding into them. Ornamentation of fine-meshed, flat ribs, bordering deep, relatively small fossae, which have a longitudinal trend in ventral half of valve; irregularly distributed on remainder. Sub-central tubercle marked by smaller or no fossae, scarcely protruding above valve surface. On some specimens, v-shaped frontal scar visible on external expression of tubercle. Prominent, clear eye tubercle at anterodorsal angle.

Hinge strongly holamphidont; anterior tooth in RV curved; median elements smooth in both valves. Inner lamella of moderate width in anterior and posterior, narrower ventrally. No vestibules. RPCs numerous (15–20 in anterior; 10–12 in posterior), unbranched; occasionally paired or grouped, generally single. Muscle scar pattern difficult to determine because of reticulation. V-shaped frontal scar distinct in some specimens, adductors not determined. Sexual dimorphism — males longer and shorter than females.
Etymology. L. *cratis* = a hurdle; a reference to the wickerwork appearance of the reticulation.

Affinities. ?*Dumontina cratis* sp. nov. differs from the type species *D. puncturata* (Bosquet, 1854) figured by Deroo (1966) in the absence of any marked dorsal marginal rib and the presence of denticulations. *D. puncturata* does not have the deep sulci which characterise ?*D. cratis* sp. nov.

?*Dumontina* sp. A

Pl. 2 figs 9, 10

Figured specimens. NMV P1134949 — Pl. 2 fig. 9; NMV P123220 — Pl. 2 fig. 10.
Dimensions. (P123220) RV: L=0.63; H=0.32.
Material. 32 specimens, Clifton Bank (very rare) and Hentys, Muddy Creek Marl, early Middle Miocene.

Brief description. Reticulate *Dumontina*-like species with spines confined to posterior margin and denticulate anterior margin. Flat-surfaced muri bound small, deep fossae. Anterior furrow crossed by narrow ribs. Reticulation covers subcentral area. Marginal spines clavellate. U-shaped frontal scar is only scar which can be discriminated. Hinge holamphidont.

Remarks. Dimensions indicate that ?*Dumontina* sp. A is not an instar of ?*Dumontina cratis* sp. nov. although the reticulation is quite distinctive and suggests possible affinities with that species, from which *?Dumontina* sp. A differs by the absence of the deep anterior sulcus, the marked posterior spinosity, and the greater taper posteriorly. The u-shaped frontal scar differs from the v-shaped scar of ?*D. cratis*. The holamphidont hinge is also less strongly developed than in ?*D. cratis* sp. nov.

Deltaleberis McKenzie, Reyment and Reyment, 1991

Deltaleberis warnei sp. nov.

Pl. 3 figs 1, 2, 3

Holotype. NMV P123224 — Pl. 3 fig. 2.
Paratypes. NMV P123223 (not figured); NMV P134950 — Pl. 3 fig. 1; NMV P134951 — Pl. 3 fig. 3.
Dimensions. Holotype RV: L=0.64; H=0.27 Paratype (P123223) LV: L=0.57; H=0.32.
Material. 43 specimens, Clifton Bank and Hentys, near Hamilton. (A closely related, and possibly ancestral, form in my collection also occurs in SA, in the early Late Eocene Tortachilla Limestone at the type section 'Uncle Tom's Cabin'.) Muddy Creek Mark, early Middle Miocene.

Diagnosis. Deltaleberis with broad transverse rounded ribs, posterior one marked by round, pitted depression; anterior by central constriction.

Description. Valves subequal; hyaline in fresh specimens. Subtrapezoidal in lateral view; elongate. Anterior broadly rounded; finely denticulate anteriorly; greatest length medially. Dorsal margin straight; posterodorsal cardinal angle approximately 135° ; posterodorsal margin straight. Posteroventral margin subrounded, with denticulations. Ventral margin slightly sinuous, concave medially. Lateral valve surface irregularly inflated in 2 transverse rounded ridges (variable from specimen to specimen). Subcentral swelling (not a tubercle). Posteroventral region compressed, bordered by rounded ridge.

Valve surface smooth on ridges (under high magnification very small pores irregularly distributed over these smooth surfaces); small punctae on other surfaces (Pl. 11 fig. 4). Punctae form clearly defined patterns giving sieve-like appearance to surface of valve. Eye tubercle indistinct and merged with transverse ridge. Muscle scars as for the genus. RPCs simple, unbranched — few (7–8) on anterior margin; more closely spaced on posteroventral margin (also 7–8). Normal pores widely scattered; simple. Line of concrescence and inner margin coincident except for anteroventral sector with small vestibule; fused zone broad anteriorly.

Hinge holamphidont, but not strongly so. Sexual dimorphism — males more elongate and less inflated than females.

Etymology. For Dr M. T. Warne, in recognition of his work on the ostracode faunas of south-eastern Australia.

Affinities. The valve surfaces of *Deltaleberis warnei*, with their ornamentation a combination of smooth inflated ribs or ridges and finely punctate interareas, are very similar to those of the type species *Deltaleberis rugosapytta* McKenzie et al., 1991. *Deltaleberis warnei* sp. nov. differs from the type species in its more elongate shape, even in females, and pattern of transverse ribs. It differs from *D. delicata* McKenzie et al., 1993 in having a straight posterior margin, different rib pattern, and notably a different style of fine ornamentation (Pl. 11 fig. 4).

Alatahermanites Whatley and Titterton, 1981

?***Alatahermanites septarca*** sp. nov.

Pl. 3 figs 4, 6

Holotype. NMV P123221 — Hentys — Pl. 3 fig. 4.
Paratypes. NMV P123222 (not figured); NMV P134952 — Pl. 3 fig. 6.
Dimensions. Holotype RV: L=0.85; H=0.40 Paratype (P123222) LV, instar: L=0.73; H=0.35
Material. 17 specimens, Hentys, Muddy Creek Marl, early Middle Miocene.

Diagnosis. Medium to large (up to 1 mm) ?*Alatahermanites*, with strongly ponticulate, 7–arched, alar ventral ridge; prominent subcentral tubercle and pitted surface ornamentation.

Description. Valves subrectangular in lateral view; somewhat elongate because of reduction in height from anterior to posterior. Dorsal and ventral margins straight. Anterior broadly and evenly rounded with greatest length at mid-height; posterior angulate, with greatest extension below mid-height, posterodorsal margin slightly concave and posteroventral margin straight. Anterior very finely denticulate; posterior with 4 or 5 spines well-developed in ventral half. Anterodorsal cardinal angle moderately defined; posterodorsal cardinal angle more so. Prominent 'hinge' tubercle (cf. Treatise p. Q339) developed at the anterodorsal angle. No eye tubercle or interior eye sinus. A dorsal rib clearly developed from anterior of sulcus behind 'hinge' tubercle to its termination short of the

posterodorsal angle; subponticulate, with no apertures in the arches. A strongly-developed rib linking the 'hinge' tubercle with the dorsum through a loop not in contact with the subcentral tubercle — the loop outlining a deep sulcus. Ventral rib very strongly developed from the anteroventral margin to its culmination in a very prominent rounded knob, projecting substantially from the lateral surface of the valve. This rib ponticulate in form with seven clearly differentiated arches.

Ornamentation: fine pattern of pits covering lateral surface of valves, large arched ribs linking body of valve to dorsal, anterior and ventral margins. (In some specimens small pits cover all surfaces except ribs and tubercles.) Hinge strongly but modified holamphidont, with very large, stepped, anterior tooth and socket, narrow median bar and small posterior tooth right on cardinal angle in RV; LV corresponding but median groove not strongly marked. The unusual anterior tooth in the LV ('conical pessular' tooth of *Idiocythere*, cf. Treatise: Q339) present in adult specimens with hingeline intact.

Muscle scars not readily resolvable. Frontal scar single, distinctly U-shaped with long arms; adductors a row of 4 with dorsal smallest and middle 2 scars very elongate; ventral scar not distinguished easily because of inner curvature of muscle scar depression (subcentral tubercle). Inner margin and line of concrescence coincide. Radial pore canals numerous, straight and unbranched on anterior margin.

Etymology. From the Latin for the seven arches characterising the ventral ridge.

Affinities. ?Alatahermanites septarca sp. nov. differs from the type species *A. hastatus* Whatley and Titterton, 1981 in its ornament, which is ponticulate on both dorsal and ventral margins, and pitted on the lateral surface, rather than the 'very strong coarse reticulation' of *A. hastatus.* Although it shares the subrectangular shape of *Alatahermanites*, its posterior is distinctive in being strongly denticulate and somewhat caudate, and there is a strong 'hinge' tubercle which is not characteristic of *Alatahermanites. ?A. septarca* shares some characteristics with *Idiocythere* Triebel, 1958 in its pitted surface ornamentation and denticulate posterior but lacks the tapered shape of that genus. The modified holamphidont hinge, diagnostic of *Alatahermanites,* also shares a characteristic with *Idiocythere*, notably the additional anterior rim tooth in the LV. On balance, tentative placement in *Alatahermanites* is preferred.

Remarks. This species is only tentatively attributed to *Alatahermanites* because of some shared features with *Idiocythere*. This occurrence implies that *Alatahermanites* may range into the Middle Miocene. Although the specimens allow the erection of a new species, the details of the hinge structure and muscle scar pattern need to be clarified with better preserved material. Many of the specimens have damaged hinge lines.

Idiocythere Triebel, 1958

Idiocythere sp.
aff. *I. thalassea* McKenzie, Reyment and Reyment, 1991

Pl. 3 fig. 5; Pl. 11 fig. 5

Figured specimen. NMV P123361 — Pl. 3 fig. 5; Pl. 11 fig. 5.
Dimensions. LV L=0.63; H=0.32.
Material. 1 specimen, Clifton Bank, Muddy Creek, near Hamilton, Muddy Creek Marl, late Early Miocene.

Remarks. One valve possibly conspecific with *Idiocythere thalassea* McKenzie et al., 1991: pl. 9 fig. 9 occurs in the fauna from Clifton Bank, Sample 10. Its hingeline is broken.

Tribe **Incertae sedis** ('Australimoosellini' Howe and McKenzie, 1989.)

Mackencythere Malz and Ikeya, 1982

Mackencythere sp. A.

Pl. 3 fig. 7

Figured specimen. NMV P123360 — Pl. 3 fig. 7.
Dimensions. RV L=0.46; H=0.22.
Material. 3 specimens, Hentys on Grange Burn, Muddy Creek Marl, early Middle Miocene.

Remarks. These specimens belong to a species of *Mackencythere* with a narrow anterior ridge and two concentric posterior ridges, a complex reticulation of narrow rounded ribs, and a marginal, reticulated posterior flange. The muscle platform diagnostic of the genus is clearly marked. *M.* sp. A differs from the type species, *M. venata* (Brady), 1866 in the absence of a median ridge and a more rounded posterior. It differs from *M.* sp. 1 Warne, 1987 in its narrower anterior ridge, its finer reticulation and its rounded, reticulate posterior.

Arculacythereinae Hartmann, 1981

Arculacythereis Hartmann, 1981

Discussion. The use of *Arculacythereis* Hartmann, 1981 for the following species is based on

the distinctive thickening of the shell wall below and behind the anterior hinge elements on the interior of the valve, and the distinctive pattern of ornamentation. The former characteristic is shared by genera such as *Australimoosella* Hartmann, 1978, *Doratocythere* McKenzie, 1967, *Waiparacythereis* Swanson, 1969 and *Yassinicythere* Howe and McKenzie, 1989 (McKenzie, pers. comm. 1989). However, the ornamentation of these genera is quite different from that of *Arculacythereis*.

?Arculacythereis postdeclivis (Chapman, 1914)

Pl. 3 figs 8, 9, 10

Cythere postdeclivis Chapman, 1914: 39–40, pl. 7 figs 23a, b.

Cytheralison postdeclivis. — McKenzie, 1981: 106.

Figured specimens. NMV P123225 — Hentys — Pl. 3 fig. 8; NMV P134953 — Pl. 3 fig. 9; NMV P134954 — Pl. 3 fig. 10.

Dimensions. (P123225) RV: L=1.08; H=0.56; W=0.29.

Material. 17 specimens, Hentys and Clifton Bank, near Hamilton, Muddy Creek Marl, early Middle Miocene.

Diagnosis. Large *?Arculacythereis* with posterior depression; thick shell; reticulation marked by a tendency for longitudinal rather than lateral alignments; bean-shaped valves with slight median 'waist' or narrowing, and divided frontal scar.

Description. Valves large, tumid, thick-walled and bean-shaped. Anterior broadly rounded and slightly recurved ventrally. Posterior also broadly rounded, with very slight caudal process in ventral half. Eye tubercle indistinct. Ornamentation of deep subcircular to oval or elongate fossae, bounded by broad, flat-surfaced muri. Reticulation pattern oriented vertically rather than laterally. Little evidence of subcentral tubercle on external surface of valves.

Muscle scars adjacent to, but not in, subcentral pit on interior surface of valves. Two frontal scars, subcircular and separate; dorsal smaller than ventral; 4 adductor scars, the dorsomedian in some specimens elongate, in others divided; ventromedian and ventral scars subequal and closely associated, or even conjoined so as to give appearance of only 3 adductors. Shell thickening below anterior hinge elements, in a slightly elongate ridge.

Hinge weakly holamphidont. Hinge elements smooth. Inner margin and line of concrescence coincident. RPCs numerous but difficult to distinguish. Sexual dimorphism — females shorter and higher than males. Juveniles with reticulation more marked, muri narrower than in adults; hinge hemiamphidont. Very large, indistinctly ornamented specimens common.

Affinities. *?Arculacythereis postdeclivis* (Chapman, 1914) shows some affinities with *Lankacythere coralloides* (Brady, 1886) from which it differs in its more ovate fossae, the absence of the ear-shaped posterior ridge and the less distinct eye tubercle (Bhatia and Kumar, 1979). However, it is on the basis of its dorsal 'stub' or ridge that the species is tentatively assigned to *Arculacythereis* rather than to *Lankacythere*, since Bhatia and Kumar make no reference to such a feature in their diagnosis of the latter genus. *Lankacythere* has a trachyleberid v-shaped frontal scar as in other campylocytherinid genera, whereas these specimens have the hemicytherid divided frontal scar consisting of two subrounded scars. To retain the species in a trachyleberidine genus raises the significance of frontal scar configuration in Trachyleberididae and Hemicytheridae.

It is possible that the assignment of *?Arculacythereis postdeclivis* (Chapman, 1914) might be confirmed when further studies of the genera *Australimoosella* Hartmann, 1978, *Yassinicythere* Howe and McKenzie, 1989, *Doratocythere* McKenzie, 1967 and *Waiparacythereis* Swanson, 1969 have been completed. At present, the significance of the anterodorsal thickening of the shell below the anterior hinge elements is equivocal, since it is also a diagnostic feature of these genera.

Remarks. Chapman's original description is inadequate. Surface ornament, hinge development and muscle scar configuration vary substantially intraspecifically. Very large thick-shelled specimens often show considerable wear and abrasion. The muri are enlarged and the fossae small and shallow — in extreme cases the surface is almost without a pattern of ornament. Bhatia and Kumar (1979) referred to variations in the form and pattern of the muri, which they suggested may be ecological. The frontal scars are occasionally joined to form one *Grinioneis*-style scar; dorsomedian adductor frequently divided also.

Arculacythereis tatei sp. nov.

Pl. 3 figs 11, 12

Holotype. NMV P123266 — Hentys — Pl. 3 fig. 11.

Paratypes. NMV P123267 (not figured); NMV P134955 — Pl. 3 fig. 12.

Dimensions. Holotype RV: L=0.78; H=0.39. Paratype (P123267) LV: L=0.70; H=0.34.
Material. 36 specimens, Clifton Bank and Hentys, near Hamilton, Muddy Creek Marl, early Middle Miocene.

Diagnosis. Arculacythereis species with reticulate/punctate ornamentation and distinct posteroventral compressed flange.

Description. Well-calcified subrectangular inflated valves, with maximum inflation on posteroventral area, bordering marked posteroventral flange. Dorsal margin straight; ventral margin slightly sinuous, subparallel to dorsal margin. Anterior very broadly rounded; posterior more narrowly rounded, with maximum lateral extension slightly above mid-height. Valve surface covered with indistinct pattern of rounded ribs, with punctae rather than fossae within the mesh of ribs. Larger, deeper fossae in arc parallel to anterior and posteroventral margins. Slight denticulations on posteroventral margin. No subcentral tubercle.

Hinge shows a thin, elongated tooth in RV. Median element appears to be smooth but difficult to determine. Only the u-shaped frontal scar visible; adductor pattern not known. Inner lamella broad in anterior, less so in posterior. No vestibules. RPCs clustered in groups of up to five; numerous; some branched. Interior of valve subdivided by swellings not matched by sulci on valve exterior. Very prominent dorsomedial projecting stub. Sexual dimorphism not evident. Juveniles show some evidence of slight sulci on external valve surface; dorsomedian stub well-developed.

Etymology. For Professor Ralph Tate who collected and described fossils from this locality in the late nineteenth century.

Affinities. Arculacythereis tatei differs from the type species *A. vacciformis* Hartmann, 1981 in having a straight dorsum, very slightly concave venter and no 'Feinskulptur', although the general pattern of ornamentation is similar. *A. tatei* is closer in shape to *A.* sp. Howe and McKenzie, 1989, but the latter is uniformly inflated, with no posteroventral flange.

Arculacythereis sp. aff. *A. thomasi* McKenzie, Reyment and Reyment, 1991

Pl. 4 figs 1, 2

Figured specimens. NMV P134956 — Pl. 4 fig. 1; NMV P123265 — Pl. 4 fig. 2.
Dimensions. (P123265) LV L=0.70; H=0.34
Material. 1 specimen, Clifton Bank, near Hamilton, Muddy Creek Marl, early Middle Miocene.

Brief description. Arculacythereis species similar to *A. thomasi* McKenzie et al., 1991 but differing in its straight rather than slightly convex dorsal margin, more compressed posteroventral area, narrower posterior and dorsal depression or pit. Because the range of intraspecific variation in *A. thomasi* is not known, the assignment is tentative.

Arculacythereinidae

Arculacythereinid gen. indet. sp. A

Pl. 4 fig. 3

Figured specimen. NMV P123268 — Pl. 4 fig. 3; NMV P123269 (not figured).
Dimensions. (P123268) LV: L=0.85; H=0.43. (P123269) RV, juvenile: L=0.71; H=0.36.
Material. 11 specimens, Hentys only, Muddy Creek Marl, early Middle Miocene.

Brief description. Arculacythereinid with deep anterior furrow; strongly inflated valve and surface ornamentation consisting of primary swellings and ribs, with fine-ribbed secondary reticulation and micropunctate surface. Anterior furrow and irregularly inflated surface reminiscent of New Zealand species *Waiparacythereis joanae* and *Waiparacythereis caudata* Swanson, 1969. Caudal development minimal differing from clear posteroventral caudae of *Waiparacythereis* species. Posterior compressed and sharply divided from medial inflated section of valve. Muscle scars include a u-shaped frontal scar, group of 4 elongate adductors and large subrounded ventral mandibular scar. Flattened dorsomedial stub projecting into interior of valve (diagnostic of arculacytherinid group of genera). Unequivocal generic assignment not possible.

Tribe **Pterygocythereidini** Puri, 1957

?Pterygocythereis Blake, 1933

?Pterygocythereis sp. indet.

Pl. 13 fig. 7

Figured specimen. NMV P123362 — Pl. 13 fig. 7.
Dimensions. LV L=0.43; H=0.28.
Material. 1 specimen, Hentys on Grange Burn, Muddy Creek Marl, early Middle Miocene.

Remarks. This specimen is a juvenile but because of the strongly developed, broad, flat-topped spines and absence of perforations and

butresses in the ventral ridge is placed in *?Pterygocythereis* rather than *Alataleberis* (McKenzie and Warne, 1986) or *Ponticulocythere* Dingle, 1981. The relationships of the genera *Alataleberis, Pterygocythereis* and *Alatacythere* were discussed by McKenzie and Warne (1986) where reference was also made to *Ponticulocythere* as a possible ancestor of *Alataleberis*. This juvenile does not provide clear evidence of any relationship with *Ponticulocythere*.

Tribe **?Pterygocythereidini** Puri, 1957

Alataleberis McKenzie and Warne, 1986

Alataleberis miocenica McKenzie and Warne, 1986

Pl. 4 figs 4, 5, 6

Alataleberis miocenica McKenzie and Warne, 1986: 38 figs 2d, 3n–r.

Figured specimens. NMV P134957 — Pl. 4 fig. 4; NMV P134958 — Pl. 4 fig. 5; NMV P123363 — Pl. 4 fig. 6.
Dimensions. (P123363) Carapace L=0.83; H=0.41; W=0.31.
Material. 32 specimens, Clifton Bank and Hentys near Hamilton, Muddy Creek Marl, early Middle Miocene.

Remarks. These specimens are clearly conspecific with those figured by McKenzie and Warne (1986) some of whose specimens came from the Clifton Bank locality. The figured specimen has a strongly developed eye tubercle, and regularly but sparsely distributed normal pores.

Hemicytheridae Puri, 1953

Hemicytherinae Puri, 1953

Tribe **Hemicytherini** Puri, 1953

Hemicythere Sars, 1925

'Hemicythere' lubrica sp. nov.

Pl. 4 figs 7, 8; Pl. 14 figs 2, 3

Holotype. NMV P123226 — Clifton Bank — Pl. 4 fig. 7, Pl. 14 fig. 2.
Paratypes. NMV P123227 — Pl. 4 fig. 8, Pl. 14 fig. 3; P123228 (Not figured).
Dimensions. Holotype RV: L=0.71; H=0.38. Paratype LV: L=0.70; H=0.41. Paratype Carapace: L=0.70; H=0.38; W=0.34.
Material. 154 specimens, Clifton Bank, near Hamilton, Muddy Creek Marl, early Middle Miocene.

Diagnosis. Smooth, shiny-surfaced, subrectangular hemicytherid, with distinct posterodorsal and posteroventral protuberances and subcentral tubercle below mid-height.
Description. Valves thick-shelled; dorsal and ventral margins straight; anterior curved but not broadly rounded; posterior with blunt caudal process in ventral half. Posterodorsal margin slightly concave. Anterodorsal cardinal angle rounded, projecting slightly above the dorsum. A hinge-ear more marked in LV than RV.

Surface smooth and shiny, with strong rounded protuberances posterodorsally and posteroventrally; former more posteriorly located than latter. Subcentral tubercle below mid-height but not strongly developed. Valve surfaces with smoothed irregularities but neither ornamentation nor ribs. Normal pores scattered over surface, type not known. Few small denticulations on posteroventral margin. Eye tubercle indistinct.

Hinge strongly holamphidont; anterior tooth in RV stepped; median bar smooth. Anteromedian tooth in LV rounded. Sockets deep. Muscle scar pattern complex and variable within the species (Pl. 14 figs 2, 3). Holotype with 2 rounded frontal scars (some specimens have 3); 4 adductors in very oblique row on side of muscle scar pit; dorsal scar small, subrounded; 2 median scars clearly divided (undivided in some specimens); ventral scar slightly elongate.

Marginal zone relatively broad in anterior and posteroventral sector; narrow vestibules. Approximately 15–20 simple, unbranched RPCs on anterior margin; few on posterior. Normal pores not observed on holotype, but possibly simple, from evidence on other specimens. Juveniles more rounded in lateral view; hinge ears not developed; hinge merodont. Sexual dimorphism not observed.

Remarks. Although the generic assignment of this species to *Hemicythere* is uncertain, it undoubtedly belongs to the tribe Hemicytherini rather than to Aurilini (Hartmann and Puri, 1974). *Hemicythere* has been recently ignored as with other genera established when an abundant and distinctive group is initially tackled. Under these circumstances the generic diagnosis tends to be too all-embracing, although in the case of *Hemicythere*, Sars' diagnosis (1922–28) remains more precise than some contemporary ones. The type genus no longer serves as a catch-all for species better related to more recently erected genera (Van Morkhoven, 1962). This scenario occurs more than once in the Hemicytheridae, e.g. Hornibrook's (1952) *Quadracythere* and *Bradleya*.

Recently fewer species have been referred to *Hemicythere* s.s. Hazel (1967) refers to the 'subreniform shape, distinctive hingement and

muscle scars' as important features characterising its type species. The assignment of '*H.' lubrica* sp. nov. to the genus needs justification in view of its subrectangular shape and absence of ventral inflation. It does not look like a *Hemicythere* species. The muscle scar pattern of the holotype, same as that of the type species, varies within the population from Muddy Creek. On the other hand, hingement is typical. '*H.' lubrica* cannot be assigned to another genus (Hartmann and Puri, 1974) even though *Hemicythere* s.s. is characteristically a Northern Hemisphere cool temperate genus.

Etymology. Latin *lubricus* — slippery; a reference to the shiny surface of the valves.

Affinities. '*H.' lubrica* has no close affinities with other species of *Hemicythere*. *Tenedocythere nuda* McKenzie et al., 1991 is similar to '*H*'. *lubrica* in lateral view and size and may even be conspecific. However, an assignment to *Tenedocythere* cannot be sustained on the basis of general shape since I believe the ornamentation and the smooth posterior tooth in RV are diagnostic and '*H*'. *lubrica* has no ornamentation and a lobed posterior tooth. On the other hand, the muscle scar pattern is given greater weight in my assignment.

'Hemicythere' tenuicostata sp. nov.

Pl. 4 figs 9, 10; Pl. 5 fig. 1, Pl. 14 fig. 4

Holotype. NMV P123230 — Clifton Bank — Pl. 4 fig. 10, Pl. 14 fig. 4.
Paratypes. NMV P123229 (Not figured); P123231 (Not figured); P134959 — Pl. 4 fig. 9; P134960 — Pl. 5 fig. 1.
Dimensions. Holotype RV: L=0.66; H=0.39. Paratype (P123229) LV: L=0.64; H=0.38. Paratype Carapace (P123231): L=0.73; H=0.41; W=0.29.
Material. 50 specimens, mostly at Clifton Bank, but also rarely at Hentys, Muddy Creek Marl, early Middle Miocene.

Diagnosis. Compressed, lightly-ridged hemicytherid, with narrow ventral flange, medially and posteriorly.

Description. Valves characteristic hemicytherid shape in lateral view, with broadly rounded anterior; slightly acuminate posterior, terminating in ventral half of valve; dorsal and ventral margins subparallel. Dorsal margin straight, with slight projections at anterodorsal and posterodorsal angles. Posterodorsal margin slightly convex and broken at midpoint by additional small projection, giving an angled profile. Ventral margin sinuous, with 2 or 3 small, widely separated denticulations towards posterior.

Surface of valves very lightly pitted in ventral half (very difficult to discern in worn specimens); narrow, horizontal ridges, very lightly developed except ventrally, and slightly radiate in the posterior. Parallel ventral ridges more marked; one ridge defining the slight ventral inflation of valves; otherwise valves compressed. No subcentral tubercle but muscle scars visible on exterior surface in some specimens. Weakly developed eye tubercle below anterodorsal cardinal angle.

Muscle scars — 4 adductors; dorsal and dorsomedian elongate (latter divided in some specimens); ventromedian and ventral scars subrounded and aligned obliquely to the trend of other adductors. Two subrounded frontal scars, ventral larger. Two clearly marked dorsal scars, anterior v-shaped, apex of v pointing anteriorly. Fulcral point between dorsal scars marked by opaque area (Pl. 14 fig. 4.)

Hinge strongly holamphidont. RV anterior tooth smooth and simple; posterior tooth narrow and blade-like, triangular in lateral view; large anteromedian socket; smooth median bar with distinct ventrally directed angulation at posterior end. LV anterior socket deep, with rounded retaining bar across ventral portion; posterior socket on posterodorsal margin, elongate and narrowed at ends; anteromedian tooth simple, smooth and rounded; median groove narrow and curved at posterior end round posterodorsal angle. Fused zone narrow, except anteriorly; inner margin and line of concrescence coincident throughout. RPCs difficult to determine. Normal pores numerous and open. Sexual dimorphism — females shorter and higher than males. No juveniles in this population.

Etymology. Latin *tenuis* — thin; *costa* — a rib; a reference to the fine, narrow ridges on the valves.

Affinities. '*H.' tenuicostata* has the characteristic hemicytherid shape and narrow ventral ridge. It differs from the type species *H. villosa* Sars, 1866 in being only lightly pitted and in its muscle scar pattern. As few Australian fossil species have been referred to *Hemicythere* (*H. tarakohensis* Hornibrook, 1952 appears to be a *Quadracythere*) '*H.' tenuicostata* has no close relationships with described species of this genus. It is markedly different in shape from '*H.' lubrica* sp. nov. Although '*H.' tenuicostata* has some points which link it to Hartmann's (1979) subgenus *Procythereis (Serratocythere)*, it cannot be placed in that taxon because its muscle scar pattern does not fit the 1–1–2–1(2) formula given

in Hartmann's diagnosis (1979); its shape is hemicytherid rather than aurilinid and it has a distinct, if small, caudal process, more noticeable in the RV. In addition, *Serratocythere* is diagnosed as foveolate ('punctate' in Sylvester–Bradley and Benson's 1971 terminology), whereas '*H.*' *tenuicostata* is only very lightly pitted.

'Hemicythere' sp. cf. *'H'. tenuicostata*

Pl. 5 fig. 2

Figured specimen. NMV P123364 — Pl. 5 fig. 2.
Dimensions. LV L=0.59; H=0.36.
Material. 22 specimens, Clifton Bank and Hentys, near Hamilton, Muddy Creek Marl, early Middle Miocene.

Remarks. This specimen is a *'Hemicythere'* similar to *'H'. tenuicostata,* but differing in more acuminate posterior, greater inflation of the valves and the posterior reticulation network.

Hemicytherid gen. et sp. indet.

Pl.13 fig. 8

Figured Specimen. NMV P123365 — Pl. 13 fig. 8.
Dimensions. LV L=0.32; H=0.17.
Material. 9 specimens, Clifton Bank and Hentys, near Hamilton, Muddy Creek Marl, early Middle Miocene.

Remarks. Although there is a characteristic ventral inflation and hemicytherid muscle scar pattern, these specimens are more elongate and acuminate than the *'Hemicythere'* species described above. Furthermore, the slightly irregular surface is punctate, rather than ridged. Assignment beyond family level is not possible.

Mackenzina gen. nov.

Type species. Mackenzina foveolata sp. nov.

Diagnosis. Hemicytherid with well-developed bifid posteroventral spine, pitted lateral surface and subacuminate cauda.

Etymology. For Dr K. G. McKenzie in recognition of his pioneering work on Australian Cenozoic ostracoda.

Remarks. Mackenzina differs from members of the Aurilini Puri, 1973. It is unlike *Mutilus* and *Aurila* in its muscle scar pattern and unlike *Pokornyella* in shape. Its double frontal scar suggests Hemicytherini Puri, 1953 and its prominent bifid spine together with other diagnostic features is regarded morphologically as warranting generic status.

Mackenzina foveolata sp. nov.

Pl. 5 figs 3, 4, 5, 6

Holotype. NMV P123235 — Hentys — Pl. 5 fig. 3.
Paratypes. NMV P123236 — Pl. 5 fig. 4; P123237 — Pl. 5 fig. 6; P134961 — Pl. 5 fig. 5.
Dimensions. Holotype RV: L=0.70; H=0.42. Paratype (P123236) LV: L=0.73; H=0.43. Paratype (P123237) RV, instar: L=0.62; H=0.36.
Material. 95 specimens, Hentys, on Grange Burn, Muddy Creek Marl, early Middle Miocene.

Diagnosis. Mackenzina with bifid posteroventral spine, small equally spaced spines on the ventral side of cauda, and regularly pitted lateral surface.

Description. Subquadrate valves; dorsal and ventral margins parallel in LV; dorsal margin slightly curved in RV; anterior gently rounded; greatest length slightly below mid-height. Posterior with subacuminate cauda slightly above mid-height of valve in lateral view. Posteroventral margin straight and angled at 315°, with 2 or 3 short, broad spines. Outer margin and outline coincident in lateral view except where bifid spine projects slightly beyond margin. Valve closure straight in dorsal and ventral view, except for slight sinus in anterior RV. Bifid character of ventral spine clearly evident in ventral view. LV overlaps RV slightly at anterodorsal cardinal angle.

Ornamentation of regular small pits over lateral surface of valves, concentric to anterior margin, but not markedly linear over the rest. Pits on base of bifid spine. Row of larger fossae above ventral ridge anterior to spine. Anterior and posterior margins compressed as generally unornamented flange. Ventral ridge extending into bifid, bladelike spine at its posterior termination, with proximal and distal components of subequal size. Small denticulations on anterior margin of less abraded specimens. Subcentral tubercle slightly below midline and in anterior of valve; free of pits; not prominent; gentle swelling only. Eye tubercle clear, distinct and glassy; well below dorsal margin in lateral view.

Inner lamella broadest anteriorly, but generally narrow. Inner margin and line of concrescence coincident (i.e. no vestibules). RPCs numerous and unbranched — more apparent in juvenile specimens. Normal pores not observed because of adherent matrix.

Muscle scars — 2 subrounded frontal scars (fused in some specimens); 4 adductors in vertical row; ventromedian scar small and sub-

circular; other adductors elongate and oblique. Sexual dimorphism not detected. Hinge strongly holamphidont; RV with strong, peg-like anterior tooth; elongate triangular posterior tooth; anteromedian socket bounded ventrally by a ridge extending from the anterior tooth; median groove smooth. LV with deep anterior socket; shallower and slightly longitudinal posterior socket; median bar faintly crenulate. Juvenile specimens with pitting around subcentral tubercle; outer areas smooth; some RPCs branched; few RPCs on cauda; bifid spine clearly developed, more acute and pointed than in adults; valve margins thinner and more flange-like; A7 instar with merodont hinge; A8 with holamphidont hinge.

Etymology. Latin — foveola, a small depression (even though the depressions may be large enough in some specimens to warrant the designation 'punctae').

Remarks. M. foveolata sp. nov. is the only species attributed to *Mackenzina,* and is most nearly related to *Hemicythere* s.s. The ornamentation of *M. foveolata* raises the question of differentiating between a smooth pitted surface and one with a reticulation of muri. Such a question becomes one to be resolved by SEM micrographs. With the light microscope, the boundaries between pits or fossae and the surrounding muri, or valve surface are critical. If the boundaries are sharp and right-angled or acutely angled and if the intervening spaces between the pits/fossae are relatively flat, the surface can be described as 'pitted' (Sylvester–Bradley and Benson, 1971). If the boundaries are less precisely defined and the intervening spaces are seen to be continuous with the sides of the fossae, the surface is reticulated (Sylvester–Bradley and Benson, 1971). In the case of *M. foveolata* sp. nov. the former applies.

Each moult represents the complete expression of the genotype for that stage provided there is enough calcite available. Greater or lesser pitting or reticulation compared with that in the adult is indicative only of the pattern for the particular juvenile stage, unless there is insufficient ambient calcite available to allow full expression. Variation does not reflect loss of some shell material through development of more pits/fossae or addition of material through the development of more muri (Roer and Dillaman, 1984). Potential for these variations to provide some palaeoenvironmental information has not been investigated.

Tribe **Aurilini** Puri, 1973

Pokornyella Oertli, 1956

'Pokornyella' sp. indet.

Pl. 6 fig. 1

Figured specimen. NMV P123368 — Pl. 6 fig. 1.
Dimensions. RV L=0.67; H=0.45.
Material. 1 specimen, Clifton Bank on Muddy Creek, Muddy Creek Marl, early Middle Miocene.

Brief description. Uuniformly punctate '*Pokornyella*' with the size of punctae decreasing from centre to margins. Truncate caudal process in the ventral half of the posterior. Prominent eye tubercle.

Remarks. Because of some similarity in shape to *Neobuntonia batesfordiense,* the specimen is only tentatively assigned to *Pokornyella.* '*Pokornyella*' sp. indet. differs from *Pokornyella australiae* McKenzie et al., 1991 in being punctate rather than reticulate. It differs from *Pokornyella* s.l. McKenzie, 1979, which is a punctate form, in its general shape, more elongate and distinctly caudate. The rarity of *Pokornyella* in these generally warm temperate to subtropical faunas is consistent with its preference for a cooler palaeoenvironment. Thus the report by McKenzie et al. (1991) of 83 from Bells Headland and Point Addis suggests some Late Oligocene cooling in south-eastern Australia. This isolated specimen is probably allochthonous.

Thaerocytherinae Hazel, 1967

Tribe **Thaerocytherini** Hazel, 1967

Hermanites Puri, 1955

Remarks. Hermanites was erected to include species from the United States and has remained a characteristic Western Hemisphere genus although its use for Eastern Hemisphere species was initially quite acceptable (Moos, 1965). Sissingh (1972) and Liebau (1975) revised European Trachyleberididae and Hemicytheridae, as a result of which species with similar external characteristics of valve shape and ornamentation formerly in *Hermanites* were reassigned to new genera. Sissingh (1972) erected *Tenedocythere* as a subgenus of *Quadracythere* on the basis of longitudinal ribbing, features of the hingement and RPCs. Liebau (1975) erected *Grinioneis* as a subgenus of *Cletocythereis,* with *Hermanites paijenborchiana* Keij, 1957 as type species. Both workers placed their genera in the Trachyleberididae in spite of difficulties in establishing a

diagnosis which incorporated frontal scars. As early as 1963 von Morkhoven recognised the potential confusion. *Hermanites* is used for species from this fauna where the original diagnosis covers their main characteristics. *Tenedocythere* and *Grinioneis* are excluded because the diagnostic characteristics of the Muddy Creek species do not fit satisfactorily.

Hermanites glyphica sp. nov.

Pl. 7 figs 3, 4, 5, 6, 7, 8; Pl. 12 fig. 4

Holotype. NMV P123249 — Hentys — Pl. 7 fig. 3.

Paratypes. NMV P123250 (Not figured); P123251 — Pl. 7 fig. 5; Pl. 12 fig. 4; P134968 — Pl. 7 fig. 4; P134969 — Pl. 7 fig. 6; P134970 — Pl. 7 fig. 7; P134971 — Pl. 7 fig. 8.

Dimensions. Holotype LV: L=0.92; H=0.59. Paratype (P123250) LV: L=0.97; H=0.59. Paratype (P123251) RV, instar: L=0.77; H=0.46.

Material. 426 specimens, Clifton Bank and Hentys, near Hamilton, Muddy Creek Marl, early Middle Miocene.

Diagnosis. Large, thick-shelled *Hermanites* with coarse, rounded reticulation, developed only in the adult form.

Description. Valves large, heavy, thick-walled; coarse reticulation. Lateral surface of valves inflated and irregular; dorsal rib short and ill-defined. Anterior margin with numerous small denticulations, often abraded. Slight caudal process below mid-line of valve, fringed by 5–6 short spines in well-preserved specimens. Eye tubercle not prominent. Subcentral tubercle high, covered by reticulation, but not large in area. Posterodorsal termination of dorsal rib a blade-like process with 2 muri of reticulation. Ventral rib terminates posteriorly in blunt process. Blade-like protuberance on ventral closure (sinus). In dorsal view carapace arrow-shaped. Characteristic semi-circular pit below subcentral tubercle, bounded by muri. Behind rim of anterior margin a row of 6–7 fossae beginning anterior to eye tubercle. Second, less-well-defined row of fossae posterior to first row and separated from it by strong rounded rib. RPCs numerous along anterior margin (25–30 straight, unbranched and occasionally paired); 8–10 RPCs on caudal process. Line of concrescence and inner margin coincident.

Muscle scars in pit internally, expressed as subcentral tubercle externally; oblique row of 4 adductors (sometimes appearing as 3, see description of *'H.' lungulata*) — dorsal long, dorsomedian dumbbell-shaped and longest, ventromedian small and circular (in some specimens drawn out, ventral slightly more extended. Two subcircular frontal scars.

Hinge holamphidont; smooth median bar; posterior tooth smooth, blade-like and at 45° to the dorsal median ridge/groove. Sexual dimorphism not clearly established; females broad and short; males relatively longer and narrower. Shell material hyaline. No signs of 'spongeous' reticulation. Juveniles do not show the strong reticulation pattern, but have fine network over finely punctate surface (Pl. 12 figs 5, 6). Juveniles all males in this population.

Etymology. Greek, *glyphe* — a carving, with reference to the appearance of the heavy reticulation.

Affinities. H. bireticulata Al-Furaih, 1980 has 3 frontal scars and differs from *H. glyphica* in its curved anterodorsal profile, absence of processes at the ends of ribs, less regular anterior ornamentation and its three frontal scars. In other respects it is fairly similar. *H. soliporosa* Al-Furaih, 1980 and *H. tranquilis* Al-Furaih, 1980 are much less rectangular and have different patterns of reticulation. *H. fungosa* Butler, 1963 has no lateral rows in the reticulation. The *H. tschoppi* (Bold, 1946) plexus has different muscle scars, regularity of reticulation and size. *H. glyphica* differs from the type species, *H. reticulata* Puri, 1953, in its less well-developed subcentral tubercle, smooth median bar in the hinge and less well-developed cauda. *H. immodica* Al-Furaih, 1984 has no mediodorsal tubercle. *H. straba* Al-Furaih, 1983 is longer and less high, with less marked reticulation. I agree with Neale's (1975) comment that *H. volans* Neale, 1975 belongs in another genus. With *H. dameriacensis* Keij, 1958 the subcentral tubercle is clear of reticulation, unlike in the case of *H. glyphica* sp. nov.

'Hermanites' thomasi sp. nov.

Pl. 7 figs 9, 10; Pl. 8 figs 1, 2; Pl. 10 fig. 9; Pl. 12 figs 7, 8; Pl. 14 fig. 6

?*Grinioneis* sp. 1. — Warne 1987: 443, pl. 3 fig. I.

Holotype. NMV P123242 — Clifton Bank — Pl. 7 fig. 9, Pl. 14 fig. 6.

Paratypes. NMV P123243, P123244 (Not figured); P134972 — Pl. 7 fig. 10; P134973 — Pl. 8 fig. 1, Pl. 12 fig. 7; P134974 — Pl. 8 fig. 2; P134992 — Pl. 10 fig. 9, Pl. 12 fig. 8.

Dimensions. Holotype LV, ♀: L=0.66; H=0.39. Paratype (P123243) RV, male: L=0.71; H=0.38. Paratype (P123244) Carapace: L=0.64; H=0.36; W=0.29.

Material. 471 specimens, Clifton Bank, Muddy Creek, near Hamilton, Muddy Creek Marl, early Middle Miocene.

Diagnosis. Small *Hermanites*-like, with well-defined subcentral tubercle and reticulation laterally radiate from it; prominent alate posteroventral process; posterodorsal spine.

Description. Valves small; LV overlapping RV slightly in anterior; dorsal and ventral margins subparallel, straight to slightly sinuous; anterior rounded; greatest lateral extension in ventral half with distinct acuminate caudal process. Three short spines on posteroventral margin; posterodorsal margin concave. Dorsal margin with small anterior 'hinge ear' on both valves. Eye tubercle distinct and clearly below dorsal margin.

Ornamentation a clear reticulation of broad rounded muri bounding narrow, deep fossae; reticular pattern laterally radiate from smooth, rounded subcentral tubercle. Muscle scars visible on external surface of tubercle. Strong ribbing on ventral surface of alar processes. Ventral rib strong. Anterior margin marked by rounded rib. Small dorsal rib terminated posteriorly by strong, projecting angular node.

Hinge holamphidont; median bar smooth. Muscle scar pattern (Pl. 14 fig 6.) a cluster of 3 frontal scars, all subcircular, 2 larger, with smaller one between. Obliquely vertical row of 4 adductor scars; dorsomedian clearly divided; posteromedian elongate. Two dorsal scars above main cluster. Muscle scar pattern substantially consistent throughout population.

Inner margin and line of concrescence coincident. Fused zone relatively narrow. RPCs and normal pores not observed. Sexual dimorphism marked; males longer and less high than females. No juveniles present in this population.

Etymology. For Dr G. A. Thomas, who assisted in the supervision of this project.

Remarks. Although the muscle scar pattern is consistent throughout the population and differs from the two frontal scars diagnostic for *Hermanites* s.s., *H. thomasi* is tentatively placed in this genus for reasons similar to those set out below for '*H.*' *lungulata*. The muscle scar pattern is characteristic of the auriline genera *Mutilus* and *Aurila* but the hingement of *H. thomasi* lacks the notched posterior tooth and stepped anterior tooth of aurilinids, and its shape in lateral view is quite unlike their ventrally inflated forms. The specimen figured by Warne (1987) is probably conspecific with '*H*'. *thomasi* but its frontal scar pattern rules out the trachyleberid *Grinioneis*. Although '*H*'. *thomasi* has a linear reticulation pattern, it is quite unlike Sissingh's (1972) figures of *Tenedocythere prava* (Baird, 1850), *T. mediterranea* Ruggieri, 1962 and *T. salebrosa* Uliczny, 1969 in that it has a subcentral tubercle free of reticulation, and its muri are somewhat flat-surfaced. Assignment to *Tenedocythere* is inappropriate.

There are some similarities to *Margocythere* McKenzie et al., 1991 but the absence of the eponymous broad margin, the smooth, rather than 'rugged' reticulation, and relatively small size rule out assignment to that genus. According to Hartmann and Puri (1974: 35) frontal scars are indeterminate between trachyleberids and hemicytherids but I place this species in Hemicytheridae, not only on the basis of frontal scars but also because of similarity to such non-trachyleberids as the bradleyine genera. On the basis of muscle scars alone, the species might be assigned to the Aurilini but it does not have auriline ventral inflation, nor the notched posterior and stepped anterior teeth of auriline hingement.

'*Hermanites*' *lungulata* (McKenzie, Reyment and Reyment, 1991)

Pl. 6 figs 9, 10; Pl. 7 figs 1, 2; Pl. 14 fig. 7

Bradleya lungulata McKenzie et al., 1991: 162, pl. 6 fig. 8, pl. 10 figs 9, 10.

'Bradleya' lungulata. — McKenzie et al., 1993: 113, pl. 7 fig. 13, pl. 8 fig. 19.

Figured specimens. NMV P123245 — Pl. 6 fig. 10, Pl. 14 fig. 7; P123246 (Not figured); P123247 — Pl. 7 fig. 1; P123248 (Not figured); P134966 — Pl. 6 fig. 9; P134967 — Pl. 7 fig. 2.

Dimensions. (P123245) RV: L=0.84; H=0.43. (P123246) LV: L=0.91; H=0.48. (P123247) Carapace: L=0.90; H=0.43; W=0.64. (P123248) LV, instar: L=0.66; H=0.35.

Material. 68 specimens, Hentys and Clifton Bank, near Hamilton, Muddy Creek Marl, early Middle Miocene.

Brief description. Medium to large *Hermanites*-like species with 'spongeous' or celated reticulation; regular lateral surface reticulation bounded by narrow, flat-surfaced muri; prominent subcentral tubercle, free of reticulation.

Affinities. This species is close to *H. (Grinioneis) paijenborchiana* (Keij, 1957) in terms of reticulation and shape, but specimens from Muddy Creek differ in having three subcircular frontal scars. It differs from other *Hermanites* as discussed below for *H. glyphica*, in having only small nodules at the ends of the dorsal and ventral ribs. It is also close to *Quadracythere*

quadrazea Hornibrook, 1952. It appears quite similar to *Limburgina quadrazea* (Hornibrook) (Benson, 1972: pl. 1 fig. 6), which specimen is quite large (L=0.93 mm), and lacks a cauda and the strong ventral ridge of *'Hermanites' lungulata*. Pl. 6 fig. 8 of McKenzie et al. (1991) differs from the other illustrated specimens in having reticulation on the subcentral tubercle, in its pattern of reticulation without clearly defined concentric sequence of reticules around the tubercle and in the rounded surfaces of the muri.

Remarks. *'H' .lungulata* is tentatively included in *Hermanites* because of its shape, caudal process, dorsal and ventral alate ventral ribs. However, its muscle scar pattern is somewhat anomalous in having three frontal scars (Muddy Creek specimens only) and two ventral adductors so closely associated that they sometimes appear as one undivided scar (Pl. 14 fig. 7). These variations are within the range of hemicytherids (Hartmann and Puri, 1974) and further underline the need for caution in using muscle-scar patterns as diagnostic at the generic level in "transitional" hemicytherids.

The use of the term 'divided' to describe a muscle scar is ambiguous. It is difficult to separate single, original adductor scars divided because of evolutionary, ecophenotypic or functional trends from separate scars fused. It is equally difficult to specify separate adductor scars even if closely associated. Divisions between components associated laterally are usually regarded as dividing a single scar, whereas divisions between components closely associated vertically are not. It is not clear from the literature whether the adductor muscle attachment points reflect the separation of fibres into clusters or not but these muscles tend to be separated vertically rather horizontally. In *'H' .lungulata*, division of the closely associated scars is vertical so that it would be generally regarded that the species had four adductor scars, the ventral two very closely associated or fused. Variation occurs intraspecifically at one location, as well as between locations.

Bradleya lungalata McKenzie et al., 1991 and *'Bradleya' lungulata* McKenzie et al., 1993 cannot belong to *Bradleya* because of their distinct cauda, flat-surfaced muri, radiate reticulation pattern, relatively small reticules and smooth subcentral tubercle, none of which fits Benson's (1972) diagnosis of Bradleyinae. Consequently, this species should be re-assigned to *Hermanites* s.l.

Bradleyinae Benson 1972

Spinobradleya McKenzie, Reyment and Reyment, 1991

Spinobradleya nodosa sp. nov.

Pl. 8 figs 3, 4, 5, 6

Holotype. NMV P123252 — Clifton Bank — Pl. 8 fig. 3.
Paratypes. NMV P123253, P123254 (Not figured); P134975 — Pl. 8 fig. 4; P134976 — Pl. 8 fig. 5; P134977 — Pl. 8 fig. 6.
Dimensions. Holotype LV: L=0.83; H=0.45 Paratype (P123253) RV: L=0.81; H=0.43. Paratype (P123254) LV, instar: L=0.63; H=0.36.
Material. 337 specimens, Hentys on Grange Burn, and Clifton Bank on Muddy Creek, near Hamilton, Muddy Creek Marl, early Middle Miocene.

Diagnosis. Subrectangular *Spinobradleya* with strongly developed blade-like dorsal and ventral ridges; finely divided reticulation with nodes developed at intersections of ridges; reticulation and nodes covering subcentral tubercle.

Description. Valves subrectangular, with dorsal and ventral margins parallel; anterior broadly rounded; posterior with small caudal process in ventral half; posterodorsal margin slightly concave. Dorsal margin in lateral view broken by division into 2 blade-like ridges. Ventral ridge developed posteriorly into alar process terminating in small node.

Ornamentation a small-meshed reticulation, with nodes at intersections. (Great intraspecific variation in the development of these nodes.) Reticulation and nodes continue over prominent subcentral tubercle. Anterior margin with ridge-like flange bearing small denticulations. Ornamentation developed on venter, and bounded by ridges and margins of alar process.

Muscle scars — 2 subcircular frontal scars, dorsal smaller; 4 adductor scars, dorsal ovate, remaining 3 elongate; ventromedian and ventral scars closely associated, but separate. Normal pores clearly visible on interior of valve (type unknown) — equally spaced and related to reticulation mesh. Line of concrescence and inner margin coincident. RPCs on anterior margin but not clearly visible.

Hinge strongly holamphidont, with anterior tooth in RV stepped. Median bar finely crenulate. Sexual dimorphism — males longer and less high than females. Juveniles develop spiny nodes before the reticulation mesh.

Etymology. Referring to the nodes on the muri of the reticulation.

Remarks. The development of nodes in the ornamentation and the muscle scar pattern are characteristic of this genus. *Spinobradleya nodosa* differs from the type species *S. acantha* McKenzie et al., 1991 with its interspine reticulation rather than separate spines; its more strongly developed subcentral tubercle and the absence of dorsal spines. It is more similar to *S. echinata* McKenzie et al., 1993 which has interspine reticulation but differs in not having the posterior flattening. *S. nodosa* is not placed in *Jugosocythereis* Puri 1957 in spite of the reticulation and nodes being noticeably developed on the subcentral tubercle. There is no development of longitudinal ridges or of the 'bridge' structure regarded as phylogenetically significant in *Jugosocythereis* by Benson (1972). The ridges on the subcentral tubercle which McKenzie (pers. comm. 1986) and Holden (1967) regarded as diagnostic of *Jugosocythereis* are not mentioned in the original diagnosis, but implied in the name from the Latin *jugum* = a yoke or ridge. Such ridges also occur in *Tenedocythere* Sissingh, 1972.

Bradleya Hornibrook, 1952 s.s.

Remarks. The original generic concept of Hornibrook was too broadly based to remain untouched. Subsequent refinement, particularly by Benson (1972), has enabled taxonomists to discriminate among this range of deep- and shallow-water hemicytherids and to establish species with important distinctive phylogenetic and/or palaeoecologic characteristics (Whatley et. al., 1983, 1984). As a result, the generic concept of *Bradleya* is now more precise than in many other Tertiary hemicytherid and trachyleberid genera. *Bradleya* species form a small consistent element in the fauna of the Muddy Creek Marl and this enables comparisons to be made both with southeastern Australia and more widely.

Bradleya* (*Bradleya*) *praemackenziei Whatley and Downing, 1983

Pl. 8 figs 7, 9; Pl. 13 fig. 2

Bradleya praemckenziei Whatley and Downing, 1983: 381, pl. 7 figs 7-9. — Warne, 1987: 443.

Bradleya morningtonensis McKenzie and Peypouquet, 1984: 301.

Figured Specimens. NMV P123369 — Pl. 8 fig. 7; P134979 — Pl. 8 fig. 9; P134993 — Pl. 13 fig. 2.

Dimensions. (P123369) LV L=0.80; H=0.43.

Material. 10 specimens. Muddy Creek at Clifton Bank and Hentys near Hamilton. *B. (B.) praemackenziei* also occurs in Fyansford Clay, the Sherwood Marl (M. T. Warne, pers. comm., 1985) and the Balcombe Clay (McKenzie and Peypouquet, 1984); in the Gellibrand Marl at Native Hut Creek and Warrambine Creek in the Leigh R. area; in the Wuk Wuk Marls, Gippsland (characterised by a continuous median ridge) and in the Morgan Limestone at Blanchetown, SA (own collections). A related, and possibly ancestral form occurs in the Late Eocene Blanche Point Formation Perkana Member as defined in Lindsay (1985). A distinctive species in the older Tuketja Member of the same formation shows sufficient morphological similarities to *B. (B.) praemackenziei* and the related form in the Perkana Member referred to above to be investigated as part of the phylogeny of southeastern Australian bradleyines (McKenzie et al., 1991). Muddy Creek Marl, early Middle Miocene for the Hamilton specimens. Approximately the same age for those from the Fyansford Formation (Balcombe Clay), the Sherwood Marl and the Wuk Wuk Marls. Those from the Morgan Limestone may be younger.

Remarks. It is clear from Whatley and Downing's (1983) and McKenzie and Peypouquet's (1984) figures that their specimens are conspecific — they are from virtually the same locality and horizon.

Whatley and Downing (1983) found this species to be a substantial element in the Balcombian fauna from Fossil Beach, Mornington (30 individuals — 7% of total assemblage). In a smaller sample, McKenzie and Peypouquet (1984) stopped their count at 50 individuals — 15% of the assemblage. In the Muddy Creek Marl, *Bradleya* species contribute a much lower proportion, *B. (B.) praemackenziei* having only 12 confirmed specimens (0.1%). With two other species *Bradleya* contibutes only 40 specimens (0.4%). A feature of the specimens from Muddy Creek is the development of the posterior end of the ventral ridge into a flattened, spine-like process. The eye tubercle is well-developed as would be expected in a relatively shallow water form.

Some of the better preserved specimens show aggradation (sensu McKenzie and Peypouquet, 1984) but it is difficult to draw palaeoecological inferences from this because of the small number of specimens in the Hamilton sample and the difficulty of discriminating between partially aggraded specimens subject to abrasion in the post-depositional environment (possibly even remanie specimens) and those not showing aggradation per se.

Some specimens, only tentatively assigned to this species, have the eye tubercle lower than the dorsal margin in lateral view, with a narrow ridge above the tubercle. These also show an enlargement of alternate denticulations along the anterior margin into short spines. This may be more widespread but cannot be detected in the more abraded specimens. The dorsum of these specimens is often very discontinuous in lateral view.

All of these points indicate intraspecific variation only.

Bradleya (Bradleya) sp. cf. *B. kincaidiana* (Chapman)

Pl. 8 figs 8, 10

Cythere kincaidiana Chapman, 1926: 132–133, pl. 10 figs 1a–c.

Figured Specimens. NMV P123370 — Pl. 8 fig. 10; P134978 — Pl. 8 fig 8.
Dimensions. (P123370) RV: L=0.84; H=0.43.
Material. 21 specimens, Hentys and Clifton Bank, on Grange Burn and Muddy Creek, Muddy Creek Marl, early Middle Miocene.

Brief description. Caudate species with clearly-defined dorsal ridge sweeping below small eye tubercle in anterior, and separate from, but paralleled by, ridge beginning at eye tubercle and continuous with strongly developed narrow ventral ridge. These ridges have a finely punctate/reticulate surface (Pl. 13 fig. 2). Posterior termination of ventral ridge a flattened spine. This characteristic spine develops to varying degrees in this species, and also in *B. (B.) praemackenziei* and is most prominently developed in some specimens of *Bradleya (B.)* sp. A (see below). Hence it should not be regarded as diagnostic at the species level. Ventral adductor scar apparently divided, but difficult to determine with certainty.

Remarks. The species is referred to *Cythere kincaidiana* Chapman, 1926 but with reservations because of the paucity of the material. The most notable feature of Chapman's species is the posterodorsal spine. This is missing from these specimens so it is appropriate to compare them with *B. (B.) kincaidiana* which they resemble in many other respects, rather than to regard them as conspecific, even though there is interspecific (and intraspecific) variability of the posteroventral spine. These specimens differ from *Bradleya regularis* McKenzie et al., 1991 in the undulating sweeps of the dorsal and ventral ridges, though the poor preservation of the latter species makes comparison difficult. They differ from *Bradleya dickbensoni* McKenzie et al., 1991 in their more caudate shape and smaller reticulation pattern. The absence of a central longitudinal ridge distinguishes them from *Quasibradleya* species.

?Bradleya (Bradleya) sp. A

Pl. 9 fig. 1

Figured Specimen. NMV P123255 — Pl. 9 fig. 1.
Dimensions. RV: L=0.70; H=0.41.
Material. 7 specimens, Hentys and Clifton Bank, near Hamilton, Muddy Creek Marl, early Middle Miocene.

Brief description. Differing from *B. (B.)* sp. cf. *B. (B.) kincaidiana* in shape of valves in lateral view, which is closer to that of *B. (B.) praemackenziei*. Differ from latter species in presence of a median ridge in reticulation pattern. This pattern has a longitudinal trend in the dorsal half of the valve. The posteroventral termination of the ventral ridge is much less prominent than in either of the preceding species. The material is too limited for the erection of a new species, and the presence of a median ridge makes assignment to the subgenus *Bradleya* tentative.

Bradleya (Quasibradleya) Benson, 1972

Bradleya (Quasibradleya) pyxos sp. nov.

Pl. 9 figs 2, 3; Pl. 13 fig.3; Pl. 14 fig. 8

Quasibradleya sp. — McKenzie, 1979: 91–92, pl. 2 figs 6, 7.

Holotype. NMV P123257 — Clifton Bank — Pl. 9 fig. 2, Pl. 14 fig. 8.
Paratypes. NMV P123256, P123258 (Not figured); P134980 — Pl. 9 fig. 3, Pl. 13 fig. 3.
Dimensions. Holotype RV, male: L=0.76; H=0.36. Paratype (P123256) LV, male: L=0.73; H=0.38. Paratype (P123258) LV, female: L=0.77; H=0.42.
Material. 98 specimens, Clifton Bank and Hentys, near Hamilton, Muddy Creek Marl, early Middle Miocene. (The occurrence in borehole WLG38 in the South Australian Willunga Embayment recorded by McKenzie [1979] is from Early Miocene, N6.)

Diagnosis. Subrectangular *Quasibradleya* with well-developed ventral ridge, strongly developed anterior ridge linking with median ridge, anterior to subcentral tubercle, but does not continue towards the posterior.

Description. Valve subrectangular in lateral view. Anterior broadly and evenly rounded. Dorsal and ventral margins subparallel. Dorsum slightly convex in anterior half, ventral margin slightly convex overall. Posterior with small, rounded caudal process in ventral half, smoothly continuous with straight margin from posterodorsal angle. Caudal process more pronounced and angular in juvenile specimens. Lateral margins unbroken by projection of ornament or ridge.

Ornamentation of lateral surface of valves a complex reticulate pattern, with tendency to longitudinal rows of fossae. Strong, rounded anterior marginal ridge. Strong ventral ridge parallel to

ventral margin, thinner than anterior ridge, and more strongly developed in stratigraphically younger specimens. Valves strongly inflated except posteriorly — caudal area compressed. Well-defined median ridge linking anterior ridge with subcentral tubercle, but not continuing beyond. Dorsal ridge in anterior half of valve a continuation of rounded anterior ridge. From eye-tubercle to posterodorsal angle, dorsal ridge developed from reticulation immediately below eye-tubercle sinus, sweeping upward to form dorsal margin in posterior half of valve.

Greatest height through anterodorsal angle to ventral margin. Greatest length medially. Greatest width medially through subcentral tubercle. Inner lamella very broad anteriorly, with numerous straight unbranched RPCs. No vestibules. Normal pores not observed.

Hinge strongly holamphidont, with median bar and groove smooth. Muscle scar pattern — 2 subcircular frontal scars aligned obliquely to long axis of valve; 4 adductors in semicircular arc concave to anterior. Dorsal adductor large, kidney-shaped; dorsomedian adductor small; ventromedian adductor clearly divided; ventral adductor small (Pl. 14 fig. 8). Eye tubercle just below anterodorsal angle — variably preserved in the material available for study. No LV/RV overlap.

Sexual dimorphism not established. Later instars with more prominent caudal process and greater angularity in ridge pattern.

Affinities. McKenzie (1979) briefly referred to a *Quasibradleya* species from borehole WLG38 at depth 76.5 m conspecific with *Q. pyxos.* Warne (1987) listed two *Quasibradleya* species from the Melbourne Trough. Of Hornibrook's bradleyine species (1952), *B. cunazea* and *B. dictyon* come closest morphologically to *B. (Q.) pyxos* but their reticulation patterns are quite different. *Quasibradleya janjukiana* McKenzie et al., 1991 is less caudate and quadrate in shape than *Bradleya (Quasibradleya) pyxos. Quasibradleya momitea* McKenzie et al., 1993 has a subrounded posterior, and a different reticulation pattern from this species.

Etymology. From the Greek *pyxos,* a box.

Remarks. This species is placed in Benson's subgenus *Quasibradleya* even though the diagnostic median ridge does not continue from the anterior beyond the subcentral tubercle. Benson's illustrated species (*B. (Q.) dictyonites, B. (Q.) prodictyonites* and *B. (Q.) paradictyonites*) are all noticeably more elongate than *Bradleya* s.s. The elongate *B. (Q.) pyxos* shares this characteristic, which, taken together with its partial median ridge, warrants placement in the subgenus *Quasibradleya.*

Quadracythere Hornibrook, 1952

Subgenus *Quadracythere* Hornibrook, 1952

Quadracythere (Quadracythere) spica Holden

Pl. 9 figs 4, 5, 6

Quadracythere spica Holden, 1976: F24, Pl.5 figs 22, 25.

Figured Specimens. NMV P134981 — Pl. 9 fig. 4; P123263 — Pl. 9 fig. 5; P134982 — Pl. 9 fig. 6; P123262, P123264 (Not figured).
Dimensions. (P123262) LV: L=0.83; H=0.50. (P123263) RV: L=0.84; H=0.48. (P123264) LV, instar: L=0.63; H=0.38.
Material. 957 specimens, Hentys and Clifton Bank, Muddy Creek Marl, early Middle Miocene.

Remarks. Holden (1976) tentatively linked his three species of *Quadracythere* from the Midway Island drillholes into an evolutionary sequence, beginning with *Q. (Q.) spica,* continuing with *Q. aequabilis* Holden, 1976 and ending with *Q. trijugis* Holden, 1976. He also suggested that marked variation in the posteroventral and posterodorsal tubercles is an ecophenotypic response (Holden, 1976: F24). Specimens of *Q. (Q.) spica* from the Muddy Creek Marl show evidence of these variations, but all are sufficiently similar to be one species. A range of instars from A6 to A8 are present with adult forms. *Q. (Q.) spica* is the most abundant species overall being the most abundant at Clifton Bank and the second most abundant at Hentys. It resembles Hornibrook's New Zealand *Quadracythere* species and is closest to *Q. mediaruga* Hornibrook, 1952, differing in the absence of the median ridge. The age of the Midway Island specimens is given as Lower Miocene, allowing time for probable migration westwards across the Pacific. *Quadracythere singletoni* McKenzie et al., 1991 lacks the longitudinal development of ribs and the prominent posterodorsal 'ear' characteristic of *Q. (Q.) spica.*

Hornibrookellina subgen. nov.

Type species. Hornibrookellina hentyensis sp. nov.

Diagnosis. Quadracythere with subrectangular valves in lateral view; posterodorsal margin not markedly caudate; shell surface strongly reticulate with no median ridge, but dorsal and ventral ribs developed to a greater or lesser extent.

Muscle scar pattern variable, but upper adductor scars undivided, and 2 frontal scars subcircular in form.

Remarks. This subgenus has been erected because of disparities between *Hornibrookella* (sensu Al-Furaih, 1977) and *Quadracythere (Hornibrookella)* Moos, 1965 s.s. The latter was erected on the basis of differences of the LV, hinge features and muscle scars from the original genus. *Quadracythere* s.s. has been used less than it might had not Hornibrook's (1952) inclusion of 11 rather widely different species extended its variability beyond present taxonomic acceptability. Material of *Quadracythere* s.s. in this fauna provides scope for a resolution of the problems associated with diagnosis and placement of *Hornibrookella* and other quadracytherid species which do not fit readily into the existing taxonomy.

The subgenus *Q. (Hornibrookella)* was erected to include distinctly quadracytherid species, including *Q. anna* (Lienenklaus, 1894) as type species. Subsequently Al-Furaih (1975, 1977) rejected Moos's diagnostic muscle scar features because he was able to show that intraspecific (and even RV and LV) variation occurred. Instead, Al-Furaih (1977) elevated *Hornibrookella* to genus level with a diagnosis focussed on shape, ridge and reticulation pattern, eye- and subcentral-tubercles and hinge. The last three characteristics are not diagnostic but are shared with *Quadracythere* s.s. To establish a genus (as distinct from a subgenus) on the basis of valve shape and a single characteristic of the reticulation pattern is debatable.

Furthermore, Al-Furaih's concept of *Hornibrookella*, thus defined, does not clearly accommodate its type species which has a definite posterodorsal extension with evidence of relatively large denticulate projections. In fact, all the species figured by Moos (1965) — *Q. (H.) anna, Q. (H.) macropora gamma,* and *Q. (H.) vahrenkampi* — share this shape, whereas the species figured by Al-Furaih (1975, 1977, 1980) and by Siddiqui (1971) have a less well-defined posterodorsal extension. If one were to look for confirmation of Al-Furaih's concept of *Hornibrookella* in eye- and subcentral-tubercles and hinge, one would find it difficult to differentiate between *Hornibrookella* and *Quadracythere* s.s.

It is clear that Moos's (1965) subgenus *Q. (Hornibrookella)* and Al-Furaih's (1977) concept of it differ, if not on muscle scar patterns, then on shape, since species of the latter are longer and less high than the characteristic quadracytherid. Both Al-Furaih and Siddiqui failed to describe muscle scar patterns of the species they included in *Hornibrookella* because of poor preservation or because they made only general statements (Al-Furaih, 1983). However, because the material fits Al-Furaih's group and because its muscle scar pattern is distinct from those of the Moos group and is consistent in occurrence, a separate subgenus can be erected for them. This leaves *Q. (Hornibrookella)* as originally diagnosed by Moos (1965) for at least *Q. (H.) anna* (Lienenklaus, 1894) (type species), *Q. (H.) macropora macropora* (Bosquet 1894), *Q. (H.) macropora gamma* Moos, 1965 and *Q. (H.) vahrenkampi* Moos, 1965.

The following species are referred to the new subgenus:

Q. (Hornibrookellina) cyclifossata, Q. (H.) cyclopea, Q. (H.) cuspidata, Q. (H.) divergens, Q. (H.) epicelis, Q. (H.) posterisella (All Al-Furaih, 1977);

Q. (Hornibrookellina) abdulrazzaqi Al-Furaih, 1983;

Q. (Hornibrookellina) platybomus, Q. (H.) directa, Q. (H.) subquadra, sp. A. (All Siddiqui, 1971); and

Q. (Hornibrookellina) hentyensis sp. nov.

The other species listed by Siddiqui *Q. (Hornibrookella) arcana* (Lubimova and Guha, 1960) is retained in the Moos subgenus because of its shape. *Hornibrookella (?) currimundria* McKenzie et al., 1993 is also retained in *Hornibrookella* because its shape and reticulation are allied to those of the type species.

Quadracythere (Hornibrookellina) hentyensis sp. nov.

Pl. 9 figs 7, 8, 10; Pl. 10 fig. 1; Pl. 13 fig. 4; Pl. 14 fig. 9

Holotype. NMV P123260 — Hentys — Pl. 9 fig. 7, Pl. 14 fig. 9.

Paratypes. NMV P123259 — Pl. 9 fig. 10; P134983 — Pl. 9 fig. 8; P134985 — Pl. 10 fig. 1, Pl. 13 fig. 4; P123261 (Not figured).

Dimensions. Holotype LV: L=0.95; H=0.53. Paratype (P123259) LV: L=0.90; H=0.48. (P123261) Paratype RV, instar: L=0.73; H=0.40.

Material. 185 specimens, Hentys on Grange Burn, at Yulecart, near Hamilton, Muddy Creek Marl, early Middle Miocene.

Diagnosis. Thick-shelled subrectangular *Q. (Hornibrookellina)* having subpolygonal semiregular reticulation with narrow muri covering lateral surface of valves. Large depression posterior to the eye tubercle.

Description. Valves subrectangular in lateral view, with dorsal and ventral margins virtually parallel. Dorsal margin in LV straight; in RV with slight anterodorsal hinge-ear (van Morkhoven, 1962). Anterior broadly rounded, with narrow flange. Posterior margin with weakly developed caudal process, more evident in LV than RV. Anterior and posterior cardinal angles rounded. Carapace inflated posteriorly in dorsal and ventral views. No marginal denticulations.

Ornament a cellular reticulation of subpolygonal, flat-surfaced narrow muri defining deep fossae. Dorsal ridge less prominent than ventral ridge. Ventral ridge marked posteriorly by narrow rib. Subcentral tubercle covered by reticulation pattern. Little suggestion of longitudinal or lateral ridges. Fossae posterior to eye-tubercle fused into large depression. In ventral view, cellular pattern of reticulation well-developed.

Inner lamella moderately broad in anterior and posteroventral sections. No vestibules. Numerous simple, unbranched RPCs, concentrated in anterior and posteroventral sections. Hinge strongly holamphidont, with smooth anterior and posterior teeth in RV; median element crenulate, with anterior end having a large, rounded tooth in LV, and with posterior end of median element flared into small rounded lobe. Normal pores not identifiable on exterior surface because of adherent matrix.

Muscle scars a subvertical row of 4 undivided adductors; 2 subcircular or slightly elongate frontal scars, and 2 small mandibular scars. Dorsal and dorsomedian adductor scars elongate; ventral and ventromedian adductor scars compressed, giving the appearance of a single, but divided, larger scar. (Pl. 14 fig. 9 and discussion above). Eye tubercle distinct and rounded. No conspicuous overlap of valves; line of valve closure in dorsal view straight. Sexual dimorphism evident — males longer and less high than females. Specimens of the 7th and 8th instars occur with adults. No distinctive juvenile features.

Affinities. Alocopocythere Siddiqui, 1971 and *Omaniella* Zawawi, 1985 nomen nudum share some characteristics with this subgenus, but the single v- or j-shaped frontal scar removes them from Hemicytheridae using conservative criterion. Howe and McKenzie (1989) suggested that *Alocopocythere,* which has been reassigned from Echinocytherideinae to Cytherettidae, may be transitional to some *Neocytheretta*. It seems likely, however, that *Quadracythere (Hornibrookella)* Moos, 1965, *Q. (Hornibrookellina)* subgen. nov., and *Omaniella* nomen nudum are transitional forms with shared morphology. Further investigations of the phylogeny of *Quadracythere* s.s., its subgenera, and these other genera will be necessary to distinguish clearly between them.

Of the 18 species of *Q. (Hornibrookella)* and *Q. (Hornibrookellina)* described and figured up to 1989, only *Q. (Hornibrookella) macropora* (Bosquet, 1984) ranges above the Oligocene. Most are confined to the Palaeogene. In terms of valve shape in lateral view and general pattern of ornamentation, *Q. (Hornibrookellina) hentyensis* sp. nov. comes closest to *Q. (H.) posterisella* (Al-Furaih, 1977) from which it differs in having a much less pronounced cardinal angle and a reticulation pattern which does not extend to the posteroventral margin. *Q. (H.) hentyensis* sp. nov. resembles through its cellular ornamentation the seven species described by Al-Furaih (1977, 1983) and *Q. (H.)* sp. A of Siddiqui (1971) but differs in valve shape, in details of ornamentation, and in having undivided adductor muscle scars and distinctive frontal scars.

Moos (1965), in diagnosing the subgenus *Q. (Hornibrookella),* and Al-Furaih (1975), in redescribing the type species *Q. (H.) anna,* drew attention to the variable muscle scar pattern, even within one species, so that it is unwise to use it as a diagnostic feature unless its consistency can be established with a hypodigm (Simpson, 1940) of at least 20 specimens. In the case of *Q. (H.) hentyensis* sp. nov. no such variation was evident in a hypodigm of 24 adult specimens (in the original collection — 20 more specimens added since then), or in a possibly conspecific population from the Wuk Wuk Marl of Gippsland (own unpublished data). To establish the phylogenetic relationships of these species, and of the genera and subgenera *Quadracythere* s.s., *Q. (Hornibrookella), Q. (Hornibrookellina)* and *Omaniella* nomen nudum, it is likely that classification by ornamentation pattern proposed by Liebau (1971) and Neale (1975) with modifications suggested by Al-Furaih (1977) will be valuable.

Etymology. From the locality 'Hentys' on Grange Burn, near Hamilton.

Remarks. This is the first record of the subgenus *Q. (Hornibrookellina)* in Australia. An undescribed species of the related subgenus [*?Q. (Hornibrookella)*] of Janjukian age, from Castle Cove (Upper Glen Aire Clays) also exists (McKenzie, 1985, pers. comm.). Similar forms (*Hornibrookella* sp. 1 Warne, 1987 and *Horni-*

brookella sp. 2 Warne, 1987) also occur in the Melbourne Trough in the Fyansford Clay at the Batesford Quarry, a formation of equivalent age to the Muddy Creek Marl. McKenzie et al., (1991) described and figured three species of *Hornibrookella*. Of these, *H. flexicostata* is dealt with under *Chapmanella* gen. nov. below; *H. aggradata* is not a *Hornibrookellina* because of its arched dorsum, caudate posterior and thickened ribs and *Hornibrookella* sp. (McKenzie et al., 1991: Pl. 6 fig. 7, Pl. 10 fig. 15) is possibly a *Hornibrookellina*, which differs from *H. hentyensis* in its anterior 'hinge ear' and its caudate posterior, especially marked in the specimen figured in Pl. 10 fig. 15.

Q. (Hornibrookellina) hentyensis sp. nov. occurs only at Hentys on Grange Burn and is not found in any of the samples from Clifton Bank. The species is part of the biocoenose, as juveniles of at least three instars occur with the adults. The juveniles tend to be a little less rectangular and more tapered posteriorly. Whatley and Downing (1983) did not record *Quadracythere* s.s. or its subgenera from their Balcombian locality, probably because deeper water conditions prevailed, as indicated by a fauna in which *Krithe nitida* was the most abundant species. *Q. (Hornibrookellina)* cf. *hentyensis* was also recorded from the Wuk Wuk Marl on the Mitchell River, Gippsland (Neil, 1985; unpublished data — Geol. Surv. Vic. Locality No. GSV–F31).

Urocythereidinae Hartmann and Puri, 1974

Ambostracon Hazel, 1962

'Ambostracon' recta sp. nov.

Pl. 5 figs 7, 8, 9, 10; text-fig. 3

Holotype. NMV P123270 — Clifton Bank — Pl. 5 fig. 10, text-fig. 3.
Paratypes. NMV P123271 — Pl. 5 fig. 9; P134962 — Pl. 5 fig. 7; P134963 — Pl. 5 fig. 8.
Dimensions. Holotype LV: L=0.54; H=0.28. Paratype (P123271) RV: L=0.52; H=0.29.
Material. 89 specimens, Clifton Bank only, (not present at Hentys), Muddy Creek Marl, early Middle Miocene.

Diagnosis. Small, subquadrate *Ambostracon*-like species with noded dorsal ridge having prominent posterodorsal termination.

Description. Valves subquadrate in outline; slightly tapered. Anterior broadly rounded; dorsal margin with anterodorsal hinge ear, and slightly arched in RV; dorsal margin of LV with greatest height at anterodorsal cardinal angle; ridged section of valve surface projects posterodorsally as slight arch beyond otherwise straight line of margin. Posterior marked by subacuminate cauda in ventral half. Ventral margin almost straight. Ornamentation — noded rib oblique to dorsal margin from below eye tubercle to posterodorsal angle; narrow anterior ridge; concentric noded anterior and anteroventral rib; discontinuous noded ventral rib; sharply-edged wedge-shaped termination to posterodorsal lateral surface. Subcentral tubercle not strongly developed. Eye spots below anterodorsal angle of valve. Margins without denticulations except for 2 small denticles on posteroventral margin.

Hinge strongly holamphidont. LV median bar slightly crenulate on margin. Teeth on RV smooth. Posterior tooth and socket at posterodorsal angle and extended linearly around that angle. Muscle scar pattern of 3 frontal scars, 1 small and anterior to 2 larger ones; adductor scars subdivided in a distinctive array (text-fig. 3). Inner lamella moderately broad anteriorly; narrower posteroventrally. RPCs numerous, simple and straight. Normal pores not observed.

Etymology. From the L. *rectus*, right, perpendicular to the base, straight — a reference to the unusually quadrate appearance of this species.

Remarks. The species is only tentatively assigned to *Ambostracon* because of the absence of ribbed, reticulated ornamentation. McKenzie (1967) referred to *Ambostracon* species as "characterized externally by an ornament of heavy ribs and intermediate reticulations". However, its muscle scars, eye spot and hingement fall within the genus. It differs from *A. pumila* (Brady, 1866) in its more elongate shape and absence of ornamentation referred to above. Some figured species of *Ambostracon* (*A.? fredbrooki* Milhau, 1993; *A.* cf. *A. pumila* (Brady, 1866) in Swanson (1979) show little of the pattern of ornamentation referred to in Hazel's (1962) diagnosis but I stress its significance by only tentatively referring this relatively unornamented species to the genus. I agree with Dingle (1992), who regarded *Ambostracon* as a senior synonym of *Patagonacythere* Hartmann, 1962, some characteristics of which are shared by *'A.' recta*. The absence of the diagnostic areas of attachment of the inner lamella ('pillar structures') rules out assignment of *'A.' recta* to *Caudites*.

Chapmanella gen. nov.

Type species. Cythere flexicostata Chapman, 1914.

Diagnosis. Urocythereinid usually with 3 frontal

scars; a thick, rounded, marginal anterior ridge; ornamentation of longitudinal, celated, coarse ribs, and distinct caudal process in ventral half of the posterior.

Etymology. For Frederick Chapman who described the type species.

Remarks. Chapmanella shares some characteristics with *Urocythereis* Ruggieri, 1950, namely its muscle scar pattern, heavily calcified valves and strong and celated pattern of ornamentation. However, it differs in its longitudinal ribbing and its more distinct cauda.

Chapmanella flexicostata (Chapman, 1914)

Pl. 10 figs 2, 3, 4, 5, 6, 7, 8; Pl. 13 figs 5, 6

Cythere flexicostata Chapman, 1914: 35–36, pl. 7 figs 14a, 14b. — McKenzie, 1974: 160.

(?Bradleyini) gen. C, *flexicostata* (Chapman). — Warne, 1987: 443.

Hornibrookella flexicostata. — McKenzie et al., 1991: 159-160, pl. 10 fig. 11.

Figured specimens. NMV P123371 — Pl. 10 fig. 7; P134986 — Pl. 10 fig. 2; P134987 — Pl. 10 fig. 3; P134988 — Pl. 10 fig. 4, Pl. 13 fig. 6; P134989 — Pl. 10 fig. 5; P134990 — Pl. 10 fig. 6; P134991 — Pl. 10 fig. 8; P134994 — Pl. 13 fig. 5.
Nominate Specimens. NMV P123232; P123233; P123234.
Dimensions. (P123371) Male LV instar: L=0.41; H=0.22. (P123232) RV: L=0.76; H=0.42. (P123233) LV: L=0.74; H=0.41.
Material. 236 specimens, Clifton Bank and Hentys, Muddy Creek Marl, early Middle Miocene. Also recorded by McKenzie et al., 1991 from Late Oligocene to Middle Miocene, and by Warne, 1987, Early Middle to Late Miocene.

Description. In lateral view, subquadrate valves, tapered posteriorly. Dorsal and ventral margins straight in LV; dorsal margin slightly convex in RV. (Some specimens show a slight 'hinge-ear' at the anterodorsal cardinal angle in LV.) Carapace blunt arrow shape in dorsal view. Blunt caudal process in ventral half of posterior, with 3 or 4 short, peg-like spines. (Two rows of spines superimposed in some specimens.) Anterior broadly rounded, with greatest lateral extension in ventral half; numerous small denticulations — usually very abraded in the population studied. Anterior bounded by rounded, substantial ridge, continuous along ventral margin, but tapered off at anterodorsal angle. Dorsal and ventral ridges terminated posteriorly by blunt, rounded spines. (This condition may be due to abrasion in the Muddy Creek Marl specimens; Chapman's holotype is well-preserved.) Posterodorsal margin concave.

Ornamentation a series of 6 or 7 distinct lateral ribs, more or less continuous from anterior to posterior; generally sinuous and flat-surfaced. (Specimens show a wide range of rib types from sharp-edged and narrow, through rounded, to broad and flat-surfaced — Pl. 13 figs 5, 6). Dorsal ribs sharply angled below eye tubercle; ribs slightly subparallel from subcentral tubercle in posterior half of valve; rib pattern variable between specimens. Valve surface between ribs not visible because of adherent matrix. Short rib on venter not continuous with lateral ribs. Eye tubercle present in both valves; prominent, glassy and slightly below dorsal margin.

Hinge strongly holamphidont; RV anterior tooth rounded; posterior tooth lobed; median bar smooth. LV socket deep and rounded. Inner margin and line of concrescence coincident; fused zone broad anteriorly, less so posteriorly. RPCs numerous, simple and unbranched on anterior margin; less numerous on cauda and ventral margin. Normal pores visible in valve interior; numerous and aligned in channels between ribs; not observed externally; type unknown.

Muscle scars visible on subcentral tubercle externally (in some specimens). Internally, muscle scar pattern of 3 small, subcircular frontal scars in a triangular configuration; an oblique row of 4 adductors — dorsal subrounded, dorsomedian clearly divided, ventromedian elongate, ventral ovate to subrounded. (Some intraspecific variation occurs but the pattern described is by far the most common.)

Sexual dimorphism not established with the specimens from any one sample; intraspecific variation in length/height ratios within the total population may be due to sexual dimorphs. Juveniles — A7 and A8 instars; rib pattern established, but ribs fine and threadlike (Pl. 13 fig. 6); normal pores more evident externally. Hinge merodont.

Remarks. In view of the inadequacy of Chapman's description I give a full description including the muscle scar pattern which was not known to Chapman.

The characteristics referred to above constitute a clearly differentiated set which cannot readily be incorporated in any other genus of the subfamily. If the celation of the ribbing (which is the most distinctive feature) is due to an ecological response a population without such celation may be discovered. In that event, *Chapmanella* might have to be synonymised with *Urocythereis*. McKenzie et al. (1991) figured a specimen (Pl. 10 fig. 11) which is very similar to that figured in Pl. 10 fig. 7, and assigned it to *Hornibrookella*

without discussion. For the reasons set out above, their specimens would have to be included in the new genus *Chapmanella*.

Hemicytheridae incertae sedis

Neobuntonia Hartmann, 1981

Emended diagnosis. In addition to the characters listed by Hartmann, a muscle scar pattern (Pl. 14 fig. 5) of 4 adductors, subrounded or elongate; the central 2 adductors alongside each other, rather than in a subvertical alignment. Two subrounded frontal scars, the dorsal larger — vertically aligned. In some cases, dorsomedian adductor elongate, ventromedian rounded, with alignment tending to oblique rather than horizontal. Juvenile forms show considerable variation.

Remarks. Since the muscle scars were not diagnosed by Hartmann, conspecific Recent specimens from beach sand at Robe, SA, were examined. Characteristic hemicytherid scars were found and they formed essentially the same pattern as in the fossil population from Hentys and Clifton Bank. By the criteria discussed in connection with '*Hermanites' lungulata* (McKenzie et al., 1991) the two median scars would be classified as a divided scar were it not for their subrounded, and hence quite separate, configuration. Consequently, Hartmann's diagnosis has been amended to include the muscle scar pattern, and the genus is assigned to the tribe Hemicytherini.

Neobuntonia batesfordiense (Chapman, 1910)

Pl. 6 figs 2, 3, 4; Pl. 14 fig. 5

Cytheropteron batesfordiense Chapman, 1910: 300–301, Pl. 2 figs 7a–c. — Chapman 1914: 45, Pl. 8 fig. 36.

Cytheropteron batesfordiense var. *aculeata* Chapman, 1914: 46, Pl. 8 fig. 37.

Neobuntonia siebertorum Hartmann, 1981: 115, text figs 38–46, Pl. 8 figs 6–9.

Figured Specimens. NMV P123366 — Pl. 6 fig. 2, Pl. 14 fig. 5; NMV P123367 — Pl. 6 fig. 3; P134964 — Pl. 6 fig. 4.
Dimensions. (P123366) RV: L=0.92; H=0.59 ; (P123367) RV L=0.90; H=0.60.
Material. 130 specimens, Hentys and Clifton Bank, near Hamilton, Muddy Creek Marl, early Middle Miocene.

Remarks. Examination of Chapman's types of *Cytheropteron batesfordiense* Chapman, 1910 and *C. batesfordiense aculeata* Chapman, 1914 indicated that the subspecies is not warranted. Spines in some specimens is considered intraspecific variation. Examination of paratypes of *Neobuntonia siebertorum* Hartmann, 1981 found no major morphological differences between the specimens from the Miocene deposits and the Recent species. The only differences could be attributed to effects of differential preservation of the fossil specimens (e.g. foveolation of the surface was sometimes obscured). Consequently, Hartmann's species has been placed in synonymy with the Miocene species. The species is placed in *Neobuntonia,* although there are no records from the intervening period.

Neobuntonia sp. indet.

Pl. 6 fig. 5

Figured Specimen. NMV P123238 — Pl. 6 fig. 5.
Dimensions. RV: L=0.90, H=0.58.
Material. 1 specimen, Clifton Bank on Muddy Creek, Muddy Creek Marl, early Middle Miocene.

Brief description. Neobuntonia somewhat more elongate than *N. batesfordiense*. Posterior acutely rounded without caudal process. No marginal denticulations. Surface clearly foveolate, as distinct from fossil specimens of *N. batesfordiense* where foveolation is weak, and sometimes not evident in poorly preserved material.

Notocarinovalva gen. nov.

Type species. Notocarinovalva yulecartensis sp. nov.

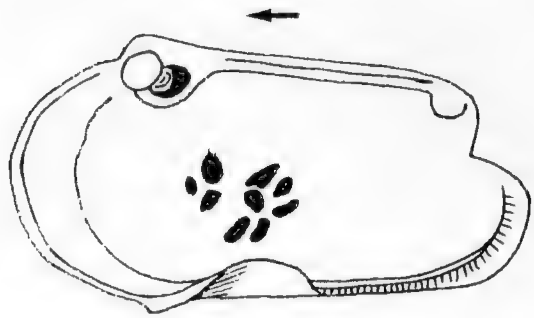
Other species. Neobuntonia airella McKenzie et al., 1991.

Diagnosis. Carinate hemicytherid with marked posterodorsal cardinal angle, and flat venter.

Etymology. Greek, *notos*, south, and *Carinovalva.*

Remarks. The type species is similar in external appearance to the type species of *Carinovalava* Sissingh, 1973 (*C. keiji* [Sissingh, 1973]), hence the generic name *Notocarinovalva*. However, significant differences between *Carinovalva* and *Notocarinovalva* include frontal muscle scars and hinge structure and lead me to assign the genus to Hemicytheridae rather than to Trachyleberididae in which Sissingh placed *Carinovalva.* The only other related species is *N. airella* (McKenzie et al., 1991).

Malz (1981a) suggested that the acceptance of a world-wide distribution of particular species and genera on the basis of external similarities is frequently in error, because separate evolutionary lines of development can be proved. It is possible that the external similarities between *Carinovalva* Sissingh *and Notocarinovalva* gen. nov.



Text-figure 3. *'Ambostracon' recta* sp. nov. NMV P123270 RV int. and muscle scars. x 100

may be due to convergent evolution, since the muscle scar patterns place the genera in different families. I believe that the external similarities of *Notocarinovalva* and *Carinovalva,* coupled with their basic difference in muscle scar pattern at the family level lend weight to this hypothesis.

Notocarinovalva yulecartensis sp. nov.

Pl. 6 figs 6, 7, 8

Holotype. NMV P123240 — Hentys — Pl. 6 fig. 6.
Paratypes. NMV P123239 — Pl. 6 fig. 8; P123241 (Not figured); P134965 — Pl. 6 fig. 7.
Dimensions. Holotype RV: L=0.71; H=0.39. Paratype (P123239) LV: L=0.71; H=0.39. Paratype (P123241) Carapace: L=0.73; H=0.43; W=0.45.
Material. 73 specimens, Hentys and Clifton Bank (rare), near Hamilton, Muddy Creek Marl, early Middle Miocene.

Diagnosis. Notocarinovalva with foveolate surface, small blunt ventral caudal process and small anterior vestibule.

Description. Valves tending to hemi-elliptical in lateral view and subequal in size. Dorsal and ventral margins straight. Anterior broadly rounded. Posterior margin slightly concave, with ventral termination marked by slight, subrounded caudal extension in line with ventral margin, and bearing some small denticulations in well-preserved specimens. Valves inflated ventrally in characteristic hemicytherid form, but bounded by rounded carinate ridge. Venter flat and broad with greatest width medially. Small anteroventral denticulations (visible only in well-preserved specimens). Small eye tubercle below valve margin at anterodorsal angle. Surface of valves foveolate in all but anterior and venter. Marginal reticulation ventrally and posteroventrally. No subcentral tubercle. Hinge strongly holamphidont in adult specimens; lophodont in juveniles. RV anterior tooth smooth; RV posterior tooth elongate; median element smooth. LV complementary.

Adductors a subvertical row of 4 individual scars — dorsomedian elongate; lower 2 scars closely associated. Two (or rarely 3) subcircular and subequal frontal scars. Muscle scars visible on exterior of valves. Small anterior vestibule. Fused zone relatively narrow. RPCs straight, unbranched and numerous only in anterior. Few thick, unbranched RPCs along ventral carina. Normal pores not observed. Sexual dimorphism not observed.

Etymology. From Yulecart, the locality in which Hentys and Clifton Bank are situated.

Affinities. Neobuntonia airella McKenzie et al., 1991 is similar to *Notocarinovalva yulecartensis* gen. et sp. nov. and should be placed in *Notocarinovalva* because it has both the marked posterodorsal cardinal angle and the flat venter diagnostic of the genus. *N. airella*, however, differs from *N. yulecartensis* in its large shallow punctations, and its less elongate shape.

Remarks. The main reason for placing *Notocarinovalva* in the Hemicytheridae is the double frontal scar. The holamphidont hinge, which lacks the special features in the hingement of *Yajimaina*, is similar to that of *Carinovalva* as figured in Sissingh (1973). See also comments on the genus.

Conclusion

The ostracode faunas of which these species form a part are dominated by the hemicytherids, though there is also a substantial representation of xestoleberids, loxoconchids, cytherurids and bairdiids. The trachyleberids and bythocytherids form a smaller proportion of the total. The prime purpose of this monograph is taxonomic, since it is on the basis of an adequate taxonomy that studies of palaeoecology and evolutionary development must be based. Other taxonomic papers are planned, to be followed by palaeoecological studies.

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Zawawi, T., 1986? Ostracoda from Oman. Unpublished M.Sc. thesis. Macquarie University, Sydney.

Plate captions

The specimens are housed in the invertebrate palaeontology collections of the Museum of Victoria, and are identified by numbers prefixed by the letters NMV P.

The following abbreviations are used: RV, right valve; LV, left valve; C, carapace; F, female; M, male; J, juvenile; ext., external; int., internal. Sample numbers for Clifton Bank are referred to in the introduction. 'Hentys' is the locality name for the bulk sample from Grange Burn (Fig. 1). Localities for the specimens are given as either Clifton Bank or 'Hentys'. The stratigraphic level of samples from Clifton Bank is given in Fig. 2. The Early - Middle Miocene boundary is between planktonic foraminiferal zones N8 and N9. In some cases, the stratigraphic level of specimens from the Clifton Bank samples is not known.

Magnifications are given for each photograph.

Plate 1

1. *?Trachyleberis robustus* (Yassini and Jones, 1987) RV ext. NMV P123216 Clifton Bank,

Sample 5 (Middle Miocene) x 65
2. *?Trachyleberis robustus* (Yassini and Jones, 1987) RV ext. NMV P134937 Clifton Bank, Sample 8 (late Early Miocene) x 90
3. *?Trachyleberis robustus* (Yassini and Jones, 1987) C dorsal NMV P134938 Clifton Bank, Sample unknown (Middle Miocene) x 60
4. *?Actinocythereis* sp. A LV ext. NMV P123221 Clifton Bank, Sample 3 (Middle Miocene) x 65
5. *?Actinocythereis* sp. A JRV ext. NMV P134939 "Hentys" (early Middle Miocene) x 80
6. *Cletocythereis caudispinosa* (Chapman and Crespin, 1928) RV ext. NMV P134939 'Hentys' (early Middle Miocene) x 90
7. *Cletocythereis caudispinosa* (Chapman and Crespin, 1928) RV ext. NMV P134940 Clifton Bank, Sample 10 (late Early Miocene) x 90
8. *Cletocythereis caudispinosa* (Chapman and Crespin, 1928) RV ext. NMV P134941 'Hentys' (early Middle Miocene) x 90
9. *Cletocythereis caudispinosa* (Chapman and Crespin, 1928) LV ext. NMV P123327 'Hentys' (early Middle Miocene) x 90
10. *Cletocythereis* sp. cf. *C. rastromarginata* (Brady, 1880) LV ext. NMV P134942 Clifton Bank, Sample 10 (late Early Miocene) x 90

Plate 2

1. *Cletocythereis* sp. cf. *C. rastromarginata* (Brady, 1880) C ventral NMV P134943 Clifton Bank, Sample 5 (Middle Miocene) x 90
2. *Cletocythereis* sp. cf. *C. rastromarginata* (Brady, 1880) LV int. NMV P134944 'Hentys' (early Middle Miocene) x 90
3. *?Ponticocythereis* sp. aff. *P. manis* Whatley and Titterton, 1981 RV ext. NMV P134945 'Hentys' (early Middle Miocene) x 75
4. *?Ponticocythereis* sp. aff. *P. manis* Whatley and Titterton, 1981 RV ext. NMV P134946 Clifton Bank, Sample 9 (late Early Miocene) x 75
5. *?Ponticocythereis* sp. aff. *P. manis* Whatley and Titterton, 1981 RV ext. NMV P123217 'Hentys' (early Middle Miocene) x 75
6. *?Dumontina cratis* sp. nov. RV int. NMV P134947 Clifton Bank, sample unknown Middle Miocene) x 90
7. *?Dumontina cratis* sp. nov. JMRV ext. NMV P134948 Clifton Bank, Sample 4 (Middle Miocene) x 90
8. *?Dumontina cratis* sp. nov. LV ext. Holotype NMV P123218 'Hentys' (early Middle Miocene) x 65
9. *?Dumontina* sp. A JLV ext. NMV P134949 'Hentys' (early Middle Miocene) x 120
10. *?Dumontina* sp. A RV ext. NMV P123220 'Hentys' (early Middle Miocene) x 80

Plate 3

1. *Deltaleberis warnei* sp. nov. RV int. NMV P134950 Clifton Bank, Sample 10 (late Early Miocene) x 90
2. *Deltaleberis warnei* sp. nov. MRV ext. Holotype NMV P123224 Clifton Bank, Sample 10 (late Early Miocene) x 90
3. *Deltaleberis warnei* sp. nov. FRV ext. NMV P134951 Clifton Bank, Sample 8 (late Early Miocene) x 100
4. *?Alatahermanites septarca* sp. nov. RV ext. Holotype NMV P123221 'Hentys' (early Middle Miocene) x 65
5. *Idiocythere* sp. aff. *I. thalassea* McKenzie, Reyment and Reyment, 1991 LV ext. NMV P123361 Clifton Bank, Sample 9 (late Early Miocene) x 85
6. *?Alatahermanites septarca* sp. nov. JRV ext. NMV P134952 Clifton Bank, Sample unknown (Middle Miocene) x 100
7. *Mackencythere* sp. A RV ext. NMV P123360 'Hentys' (early Middle Miocene) x 120
8. *?Arculacythereis postdeclivis* (Chapman, 1914) LV ext. NMV P123225 Clifton Bank, Sample 10 (late Early Miocene) x 50
9. *?Arculacythereis postdeclivis* (Chapman, 1914) JRV ext. NMV P134953 'Hentys' (early Middle Miocene) x 100
10. *?Arculacythereis postdeclivis* (Chapman, 1914) RV ext. NMV P134954 Clifton Bank, Sample 10 (late Early Miocene) x 55
11. *Arculacythereis tatei* sp. nov. RV ext. Holotype NMV P123266 Clifton Bank, Sample 2 (Middle Miocene) x 75
12. *Arculacythereis tatei* sp. nov. LV ext. NMV P134955 'Hentys' (early Middle Miocene) x 80

Plate 4

1. *Arculacythereis* sp. aff. *A. thomasi* McKenzie, Reyment and Reyment, 1991 RV ext. NMV P134956 'Hentys' (early Middle Miocene) x 80
2. *Arculacythereis* sp. aff. *A. thomasi* McKenzie, Reyment and Reyment, 1991 LV ext. NMV P123265 Clifton Bank, Sample 10 (late Early Miocene) x 85
3. Arculacythereinid gen. indet. sp. A LV ext. NMV P123268 'Hentys' (early Middle Miocene) x 65
4. *Alataleberis miocenica* McKenzie and Warne, 1986 JRV int. NMV P134957 Clifton Bank, Sample 4 (early Middle Miocene) x 80
5. *Alataleberis miocenica* McKenzie and Warne, 1986 JRV ext. NMV P134958 Clifton Bank,

Sample 4 (early Middle Miocene) x 80
6. *Alataleberis miocenica* McKenzie and Warne, 1986 C from LV side NMV P123363 Clifton Bank, Sample 5 (Middle Miocene) x 75
7. *'Hemicythere' lubrica* sp. nov. RV ext. Holotype NMV P123226 Clifton Bank, Sample 10 (late Early Miocene) x 75
8. *'Hemicythere' lubrica* sp. nov. LV int. NMV P123227 Clifton Bank, Sample 10 (late Early Miocene) x 75
9. *'Hemicythere' tenuicostata* sp. nov. MRV ext. NMV P134959 Clifton Bank, Sample 8 (late Early Miocene) x 90
10. *'Hemicythere' tenuicostata* sp. nov. LV ext. Holotype NMV P123230 Clifton Bank, Sample 8 (late Early Miocene) x 85

Plate 5

1. *'Hemicythere' tenuicostata* sp. nov. RV int. NMV P134960 Clifton Bank, Sample 4 (early Middle Miocene) x 90
2. *'Hemicythere'* sp. cf. *'H.' tenuicostata* sp. nov. LV ext. NMV P 123364 Clifton Bank, Sample 10 (late Early Miocene) x 90
3. *Mackenzine foveolata* gen. et sp. nov. RV ext. Holotype NMV P123235 'Hentys' (early Middle Miocene) x 90
4. *Mackenzina foveolata* gen. et sp. nov. LV ext. NMV P123236 'Hentys' (early Middle Miocene) x 90
5. *Mackenzina foveolata* gen. et sp. nov. JLV ext. NMV P134961 'Hentys' (early Middle Miocene) x 100
6. *Mackenzina foveolata* gen. et sp. nov. JRV int. NMV P123237 'Hentys' (early Middle Miocene) x 100
7. *'Ambostracon' recta* sp. nov. FRV ext. NMV P134962 Clifton Bank, Sample 10 (late Early Miocene) x 120
8. *'Ambostracon' recta* sp. nov. MRV int. NMV P134963 Clifton Bank, Sample 9 (late Early Miocene) x 120
9. *'Ambostracon' recta* sp. nov. FRV ext. NMV P123271 Clifton Bank, Sample 10 (late Early Miocene) x 75
10. *'Ambostracon' recta* sp. nov. MLV ext. Holotype NMV P123270 Clifton Bank, Sample 10 (late Early Miocene) x 100

Plate 6

1. *Pokornyella* sp. indet. RV ext. NMV P123368 Clifton Bank, Sample 10 (late Early Miocene) x 85
2. *Neobuntonia batesfordiense* (Chapman, 1914) FRV ext. NMV P123366 Clifton Bank, Sample 3 (Middle Miocene) x 60
3. *Neobuntonia batesfordiense* (Chapman, 1914) MRV ext. NMV P123367 Clifton Bank, Sample 10 (late Early Miocene) x 60
4. *Neobuntonia batesfordiense* (Chapman, 1914) JRV ext. NMV P134964 'Hentys' (early Middle Miocene) x 80
5. *Neobuntonia* sp. indet. RV ext. NMV P123238 Clifton Bank, Sample 9 (late Early Miocene) x 60
6. *Notocarinovalva yulecartensis* gen. et sp. nov. RV ext. Holotype NMV P123240 'Hentys' (early Middle Miocene) x 85
7. *Notocarinovalva yulecartensis* gen. et sp. nov. JRV ext. NMV P134965 'Hentys' (early Middle Miocene) x 90
8. *Notocarinovalva yulecartensis* gen.et sp. nov. LV int. NMV P123239 'Hentys' (early Middle Miocene) x 75
9. *'Hermanites' lungulata* (McKenzie, Reyment and Reyment, 1991) JMLV ext. NMV P134966 Clifton Bank, Sample 3 (Middle Miocene) x 80
10. *'Hermanites' lungulata* (McKenzie, Reyment and Reyment, 1991) RV ext. NMV P123245 'Hentys' (early Middle Miocene) x 65

Plate 7

1. *'Hermanites' lungulata* (McKenzie, Reyment and Reyment, 1991) C dorsal NMV P123247 'Hentys' (early Middle Miocene) x 50
2. *'Hermanites' lungulata* (McKenzie, Reyment and Reyment, 1991) LV int. NMV P134967 Clifton Bank, Sample 8 (early Middle Miocene) x 65
3. *Hermanites glyphica* sp. nov. LV ext. Holotype NMV P123249 'Hentys' (early Middle Miocene) x 65
4. *Hermanites glyphica* sp. nov. FRV ext. NMV P134968 Clifton Bank, Sample 4 (early Middle Miocene) x 70
5. *Hermanites glyphica* sp. nov. JRV ext. NMV P123251 'Hentys' (early Middle Miocene) x 75
6. *Hermanites glyphica* sp. nov. C ventral NMV P134969 Clifton Bank, Sample 10 (late Early Miocene) x 70
7. *Hermanites glyphica* sp. nov. RV int. NMV P134970 Clifton Bank, sample unknown (Middle Miocene) x 70
8. *Hermanites glyphica* sp. nov. JLV ext. NMV P134971 'Hentys' (early Middle Miocene) x 80
9. *'Hermanites' thomasi* sp. nov. FLV ext. Holotype NMV P123242 Clifton Bank, Sample 10 (late Early Miocene) x 80
10. *'Hermanites' thomasi* sp. nov. MRV ext. NMV P134972 Clifton Bank, Sample 5 (Middle Miocene) x 90

Plate 8

1. *'Hermanites' thomasi* sp. nov. FRV ext. NMV P134973 Clifton Bank, Sample 5 (Middle Miocene) x 90
2. *'Hermanites' thomasi* sp. nov. LV int. NMV P134974 Clifton Bank, Sample 10 (late early Miocene) x 90
3. *Spinobradleya nodosa* sp. nov. LV ext. Holotype NMV P123252 Clifton Bank, Sample 10 (late Early Miocene) x 65
4. *Spinobradleya nodosa* sp. nov. MRV ext. NMV P134975 Clifton Bank, Sample 3 (Middle Miocene) x 80
5. *Spinobradleya nodosa* sp. nov. JRV ext. NMV P134976 Clifton Bank, Sample 10 (late Early Miocene) x 90
6. *Spinobradleya nodosa* sp. nov. JRV ext. NMV P134977 Clifton Bank, Sample 10 (late Early Miocene) x 120
7. *Bradleya (Bradleya) praemackenziei* Whatley and Downing, 1983 LV ext. NMV P123369 'Hentys' (early Middle Miocene) x 75
8. *Bradleya (Bradleya)* sp. cf. *B. kincaidiana* (Chapman, 1926) JRV ext. NMV P134978 'Hentys' (early Middle Miocene) x 90
9. *Bradleya (Bradleya) praemackenziei* Whatley and Downing, 1983 JLV ext. NMV P134979 Clifton Bank, Sample 7 (Early Middle Miocene) x 65
10. *Bradleya (Bradleya)* sp. cf. *B. kincaidiana* (Chapman, 1926) RV ext. NMV P123370 Clifton Bank, Sample 10 (late Early Miocene) x 75

Plate 9

1. *Bradleya (Bradleya)* sp. A MRV ext. NMV P123255 'Hentys' (early Middle Miocene) x 85
2. *Bradleya (Quasibradleya) pyxos* sp. nov. MRV ext. Holotype NMV P123257 Clifton Bank, Sample 10 (late Early Miocene) x 75
3. *Bradleya (Quasibradleya) pyxos* sp. nov. JLV ext. NMV P134980 'Hentys' (early Middle Miocene) x 80
4. *Quadracythere (Quadracythere) spica* Holden, 1976 FLV ext. NMV P134981 Clifton Bank, Sample 3 (Middle Miocene) x 70
5. *Quadracythere (Quadracythere) spica* Holden, 1976 RV ext. NMV P123263 'Hentys' (early Middle Miocene) x 65
6. *Quadracythere (Quadracythere) spica* Holden, 1976 JLV ext. NMV P134982 Clifton Bank, Sample 10 (late Early Miocene) x 80
7. *Quadracythere (Hornibrookellina) hentyensis* subgen. et sp. nov. FLV ext. Holotype NMV P123260 'Hentys' (early Middle Miocene) x 65
8. *Quadracythere (Hornibrookellina) hentyensis* subgen. et sp. nov. RV ext. NMV P134983 'Hentys' (early Middle Miocene) x 80
9. *Quadracythere (Hornibrookellina) hentyensis* subgen. et sp. nov. JRV int. NMV P134984 'Hentys' (early Middle Miocene) x 100
10. *Quadracythere (Hornibrookellina) hentyensis* subgen. et sp. nov. MLV ext. NMV P123259 'Hentys' (early Middle Miocene) x 65

Plate 10

1. *Quadracythere (Hornibrookellina) hentyensis* subgen. et sp. nov. JRV ext. NMV P134985 'Hentys' (early Middle Miocene) x 90
2. *Chapmanella flexicostata* (Chapman, 1914) C ventral NMV P134986 Clifton Bank, Sample 4 (Middle Miocene) x 80
3. *Chapmanella flexicostata* (Chapman, 1914) MRV int. NMV P134987 Clifton Bank, Sample 4 (Middle Miocene) x 80
4. *Chapmanella flexicostata* (Chapman, 1914) JRV ext. NMV P134988 'Hentys' (early Middle Miocene) x 100
5. *Chapmanella flexicostata* (Chapman, 1914) MRV ext. NMV P 134989 Clifton Bank, Sample 10 (late Early Miocene) x 80
6. *Chapmanella flexicostata* (Chapman, 1914) RV ext. NMV P134990 'Hentys' (early Middle Miocene) x 80
7. *Chapmanella flexicostata* (Chapman, 1914) JMLV ext. NMV P123371 'Hentys' (early Middle Miocene) x 130
8. *Chapmanella flexicostata* (Chapman, 1914) RV ext. NMV P134991 Clifton Bank, Sample 4 (Middle Miocene) x 80
9. *'Hermanites' thomasi* sp. nov. FLV ext. NMV P134992 Clifton Bank, Sample 10 (late Early Miocene) x 100
10. *Spinobradleya nodosa* sp. nov. JLV ext. NMV P134993 Clifton Bank, Sample 4 (Middle Miocene) x 100

Plate 11

[All figures show detail of surface ornament at higher magnification.]

1. *Cletocythereis caudispinosa* (Chapman and Crespin, 1928) NMV P123327 'Hentys' (early Middle Miocene) x 400
2. *?Ponticocythereis* sp. aff. *P. manis* Whatley and Titterton, 1981 NMV P123217 'Hentys' (early Middle Miocene) x 375
3. *?Dumontina cratis* sp. nov. JMRV NMV P134948 Clifton Bank, Sample 4 (Middle Miocene) x 220
4. *Deltaleberis warnei* sp. nov. NMV P123224

Clifton Bank, Sample 10 (late Early Miocene) x 400
5. *Idiocythere* sp. cf. *I. thalassea* Detail of sub-central tubercle area NMV P123361 Clifton Bank, Sample 9 (late Early Miocene) x 250
6. *?Arculacythereis tatei* sp. nov. NMV P123266 Clifton Bank, Sample 10 (late Early Miocene) x 800
7. *?Arculacythereis tatei* sp. nov. NMV P134994 Clifton Bank, Sample 10 (late Early Miocene) x 450
8. *Alataleberis miocenica* McKenzie and Warne, 1986 NMV P134995 Clifton Bank, Sample 4 (Middle Miocene) x 800

Plate 12

1. *Mackenzina foveolata* gen. et sp. nov. NMV P134961 'Hentys' (early Middle Miocene) x 350
2. *Mackenzina foveolata* gen. et sp. nov. JLV NMV P134961 'Hentys' (early Middle Miocene) x 1100
3. *Neobuntonia batesfordiense* (Chapman, 1914) NMV P123366 Clifton Bank, Sample 10 (late Early Miocene) x 350
4. *Hermanites glyphica* sp. nov. NMV P123251 'Hentys' (early Middle Miocene) x 225
5. *Hermanites glyphica* sp. nov. NMV P134996 'Hentys' (early Middle Miocene) x 600
6. *Hermanites glyphica* sp. nov. NMV P134997 'Hentys' (early Middle Miocene) x 675
7. *'Hermanites' thomasi* sp. nov. NMV P134973 Clifton Bank, Sample 4 (Middle Miocene) x 800
8. *'Hermanites' thomasi* sp. nov. NMV P134992 Clifton Bank, Sample 4 (Middle Miocene) x 350

Plate 13

1. *'Hermanites' thomasi* sp. nov. Detail of sub-central tubercle NMV P134992 Clifton Bank, Sample 4 (Middle Miocene) x 350
2. *Bradleya (Bradleya) praemackenziei* Whatley and Downing, 1983 NMV P134993 Clifton Bank, Sample 4 (Middle Miocene) x 675
3. *Bradleya (Quasibradleya) pyxos* sp. nov. NMV P134980 'Hentys' (early Middle Miocene) x 350
4. *Quadracythere (Hornibrookellina) hentyensis* subgen. et sp. nov. NMV P134985 'Hentys' (early Middle Miocene) x 350
5. *Chapmanella flexicostata* (Chapman, 1914) NMV P134994 'Hentys' (early Middle Miocene) x 350
6. *Chapmanella flexicostata* (Chapman, 1914) NMV P134988 Clifton Bank, Sample 4 (Middle Miocene) x 350
7. *?Pteroygocythereis* sp. indet. LV ext. NMV P123362 'Hentys' (early Middle Miocene) x 120
8. Hemicytherid gen. et sp. indet. ?JLV ext. NMV P123365 Clifton Bank, Sample 7A (early Middle Miocene) x 160

Plate 14

Figures show muscle scar patterns, except where otherwise noted.

1. *?Trachyleberis robustus* (Yassini and Jones, 1987) NMV P123216 x 160
2. *'Hemicythere' lubrica* sp. nov. NMV P123226 x 300
3. *'Hemicythere' lubrica* sp. nov. NMV P123227 x 300
4. *'Hemicythere' tenuicostata* sp. nov. NMV P123229 x 400
5. *Neobuntonia batesfordiense* (Chapman, 1910) x 200
6. *'Hermanites' thomasi* sp. nov. NMV P123242 x 250
7. *'Hermanites' lungulata* (McKenzie, Reyment and Reyment, 1991) NMV P123245 x 225
8. *Bradleya (Quasibradleya) pyxos* sp. nov. NMV P123257 x 275
9. *Quadracythere (Hornibrookellina) hentyensis* subgen. et sp. nov. NMV P123260 x 200

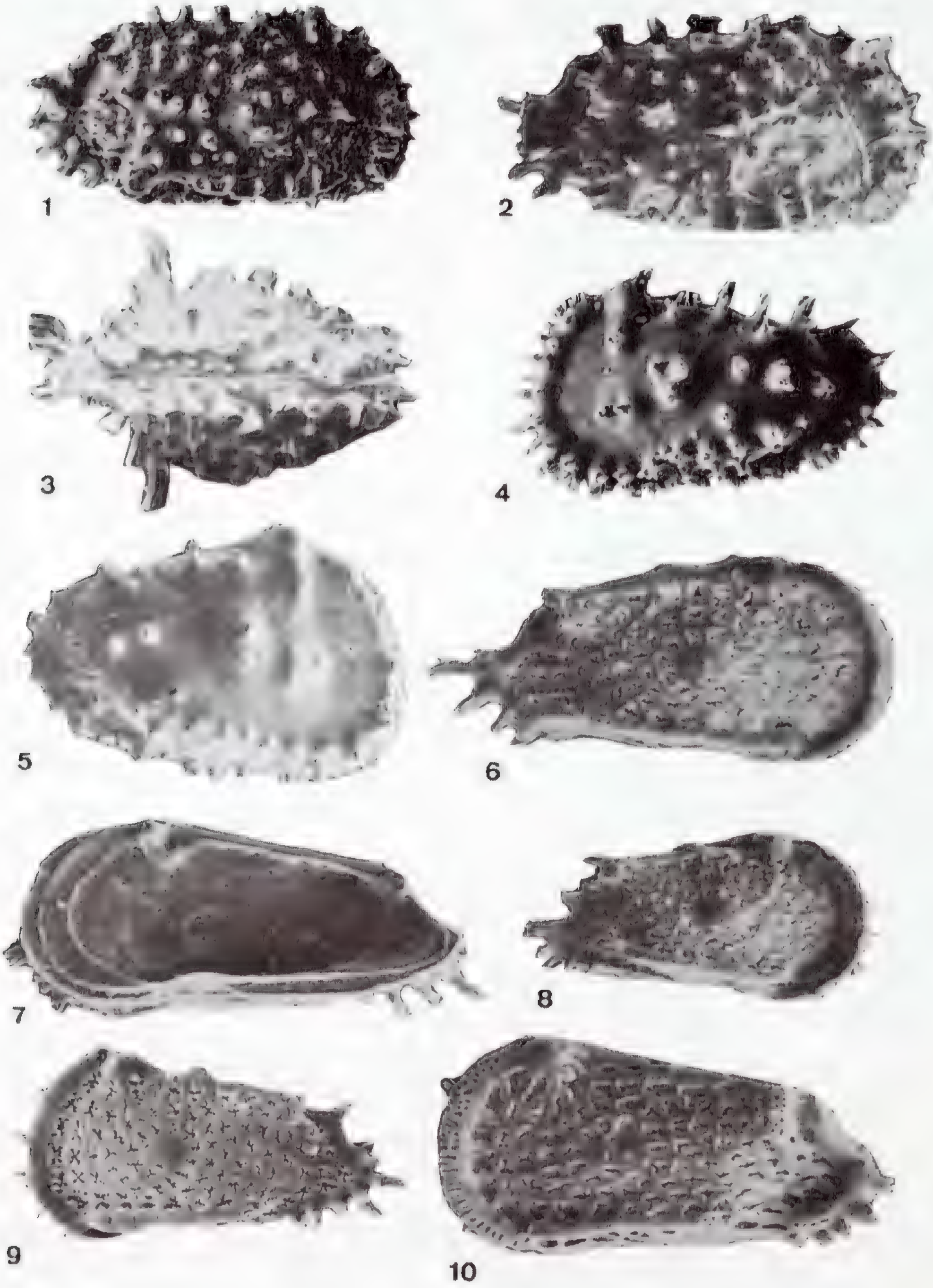


PLATE 1

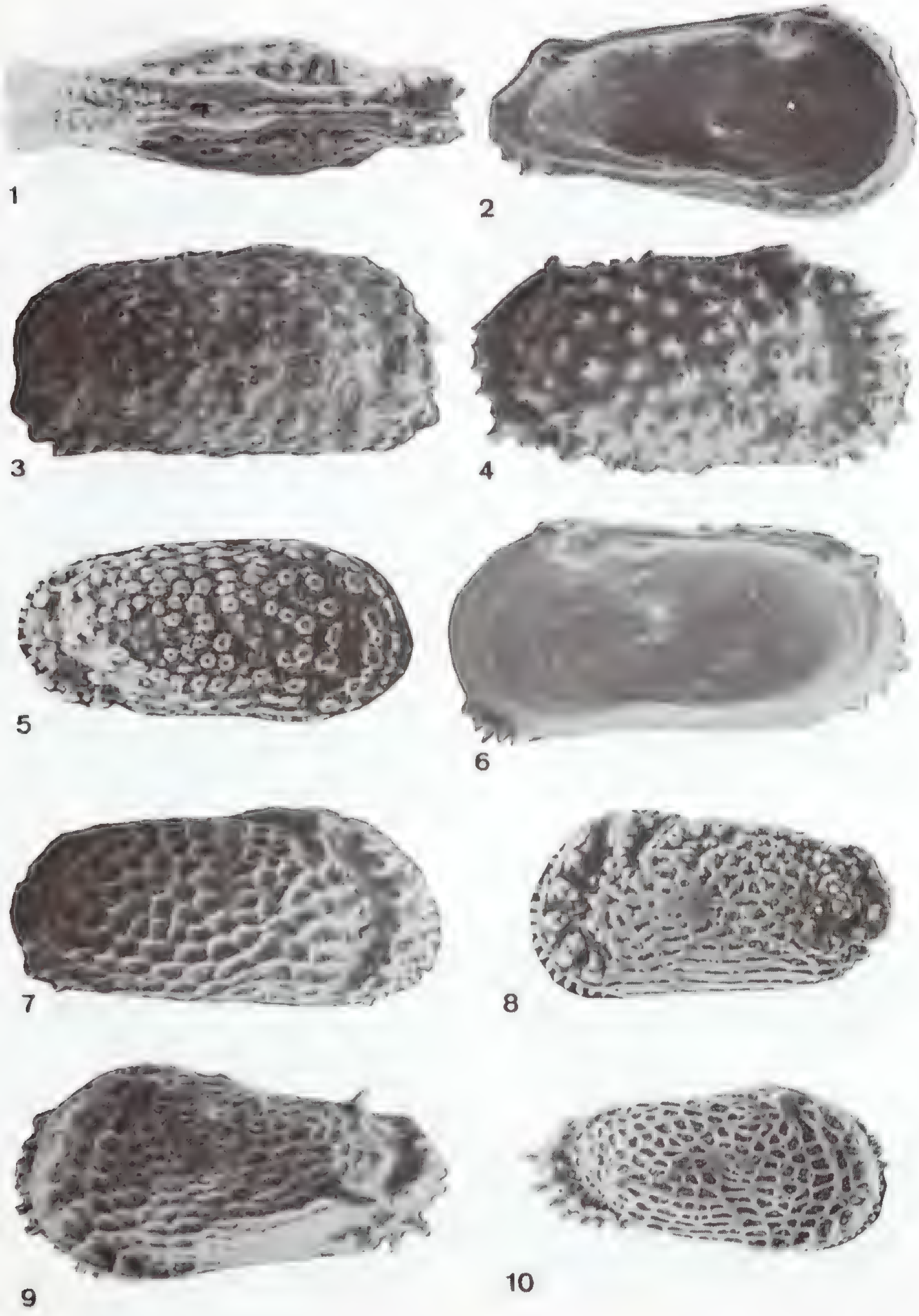


PLATE 2

PLATE 3

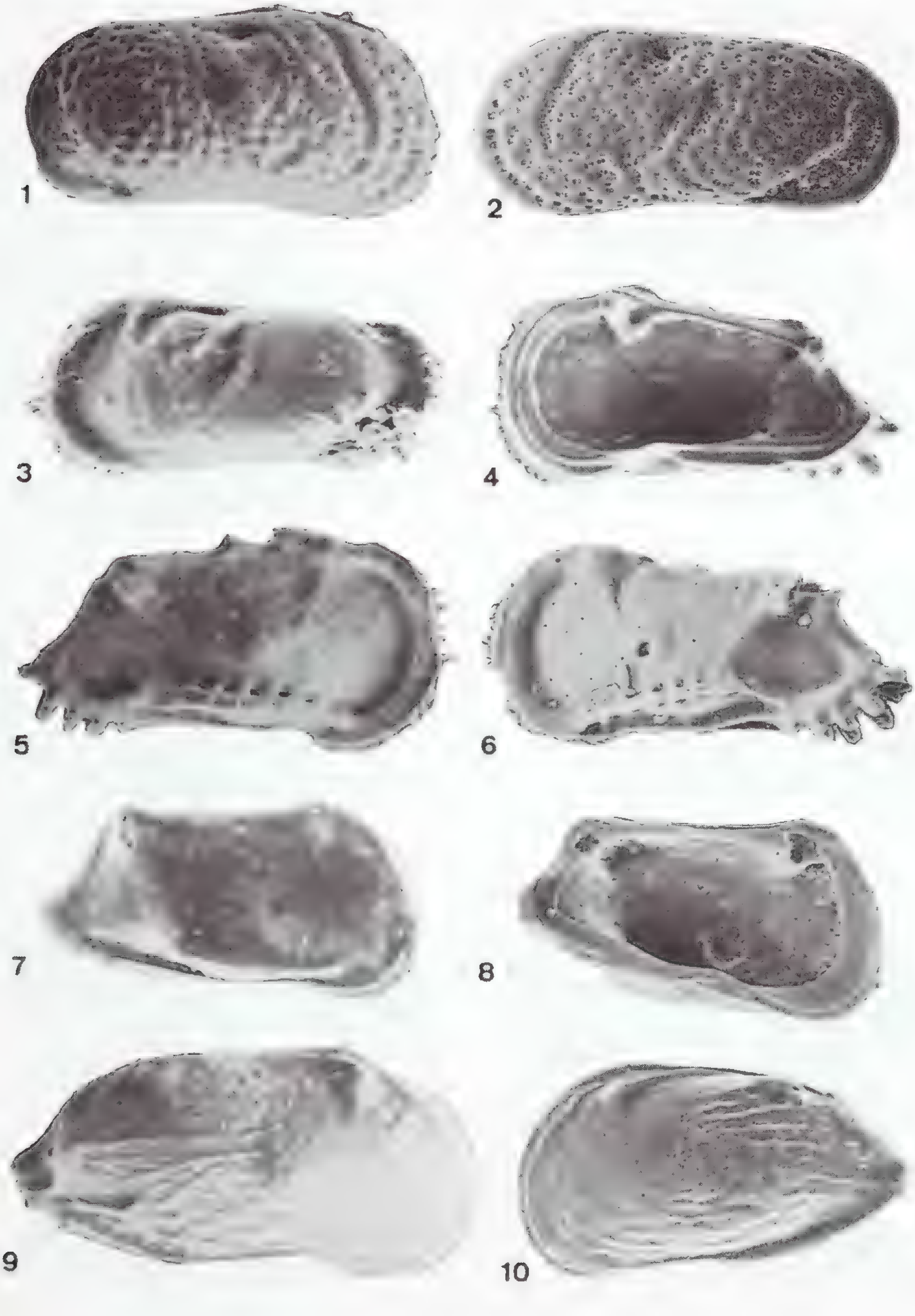
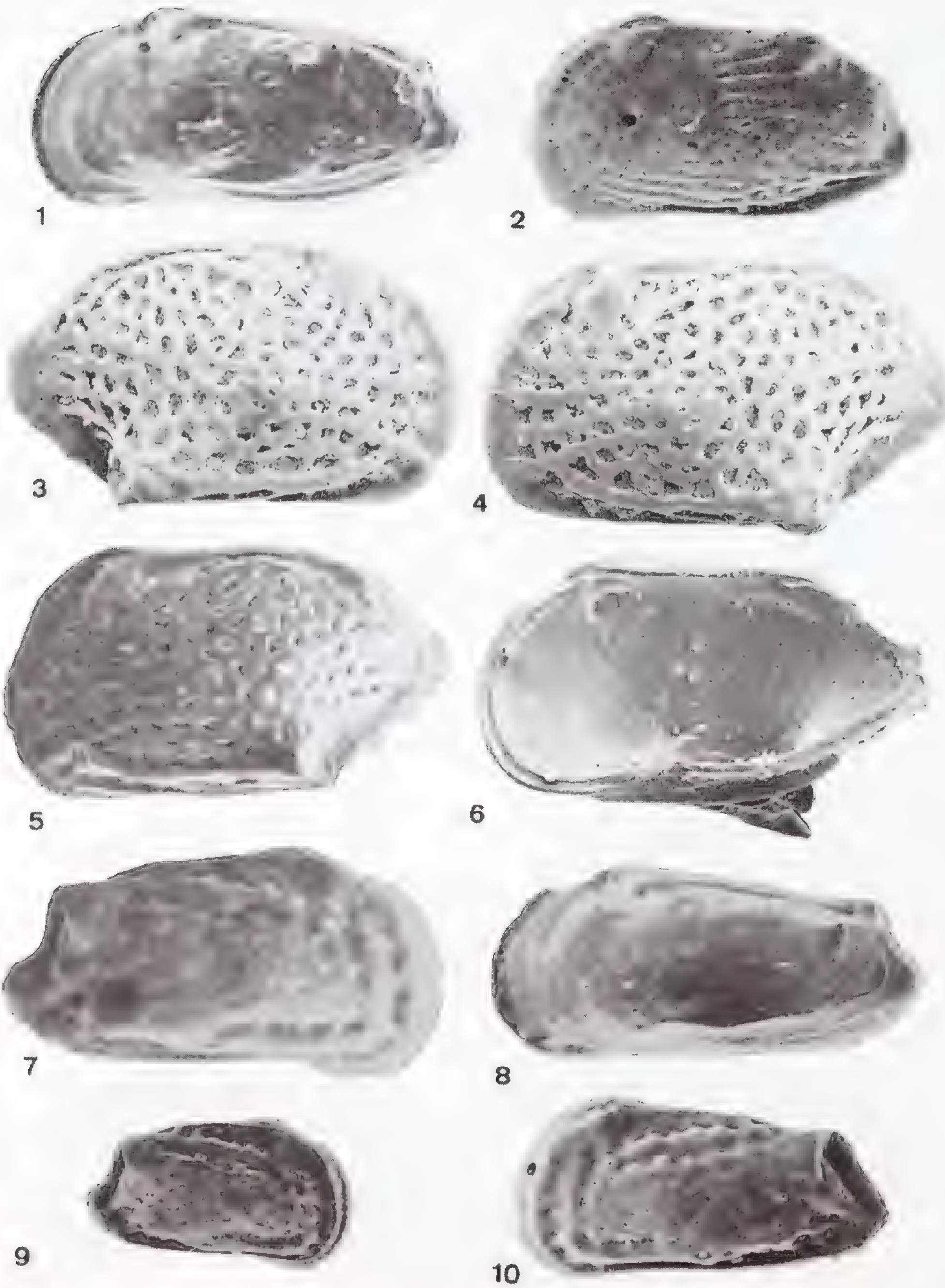


PLATE 4



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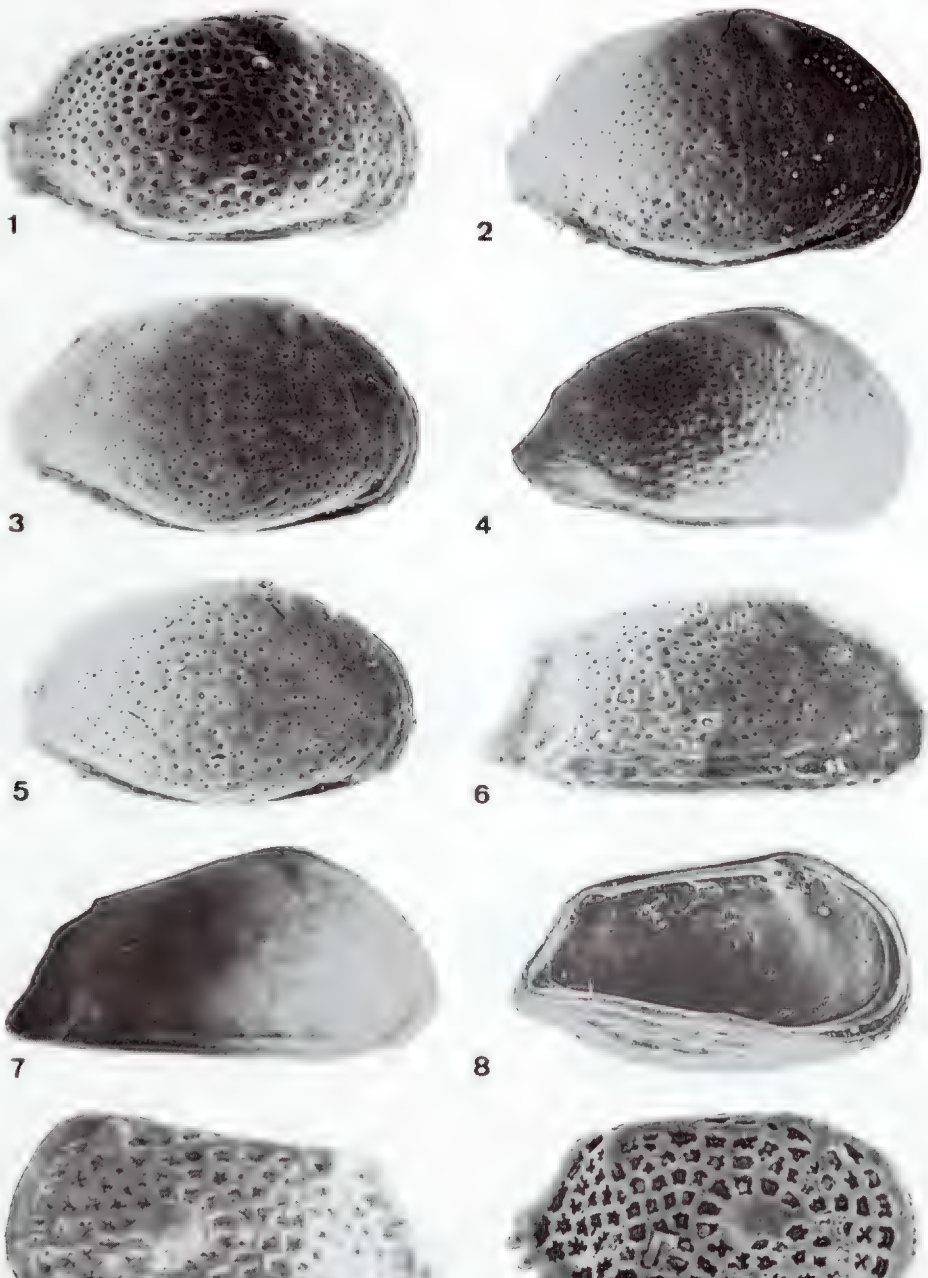

PLATE 6

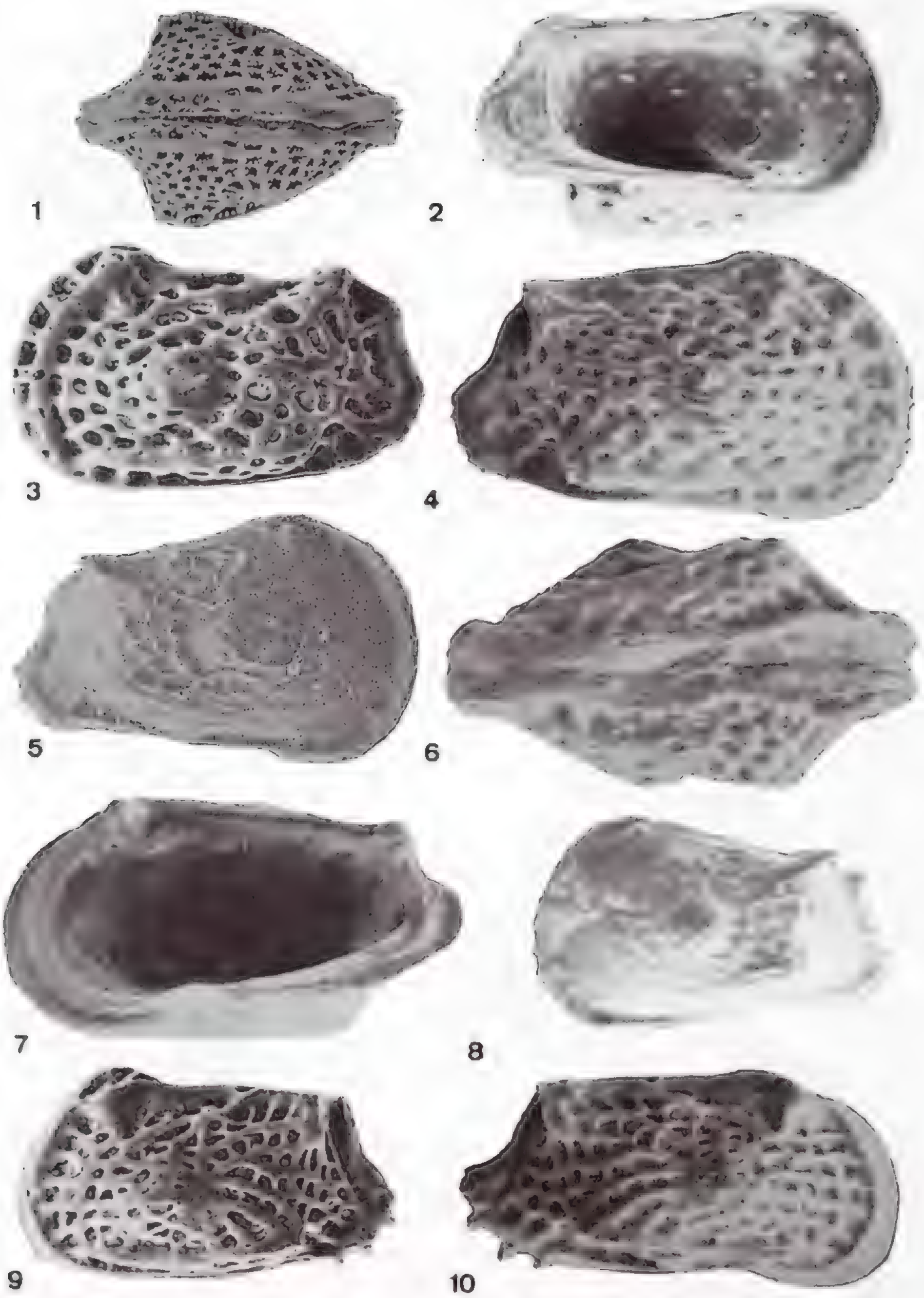

PLATE 7

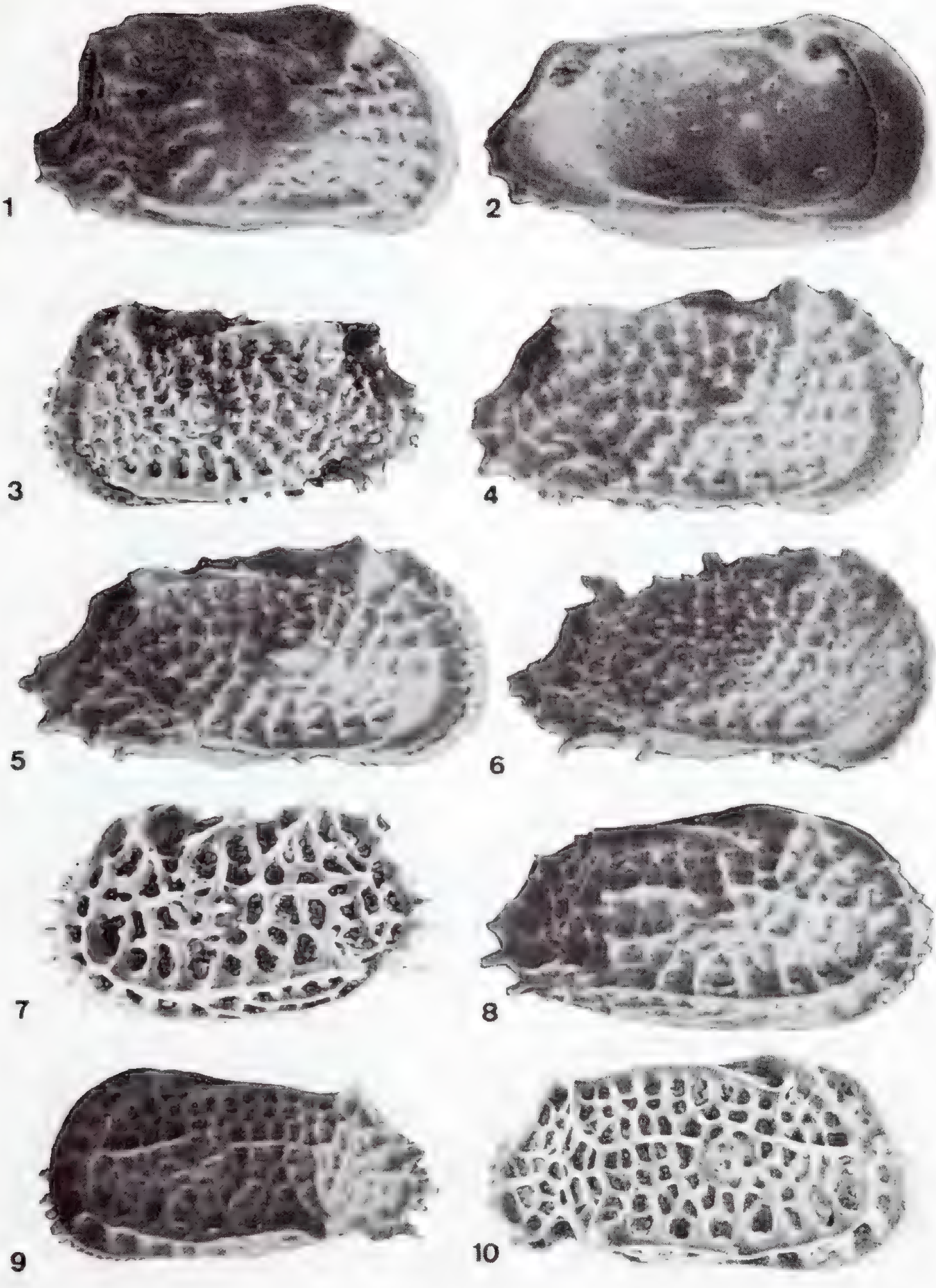

PLATE 8

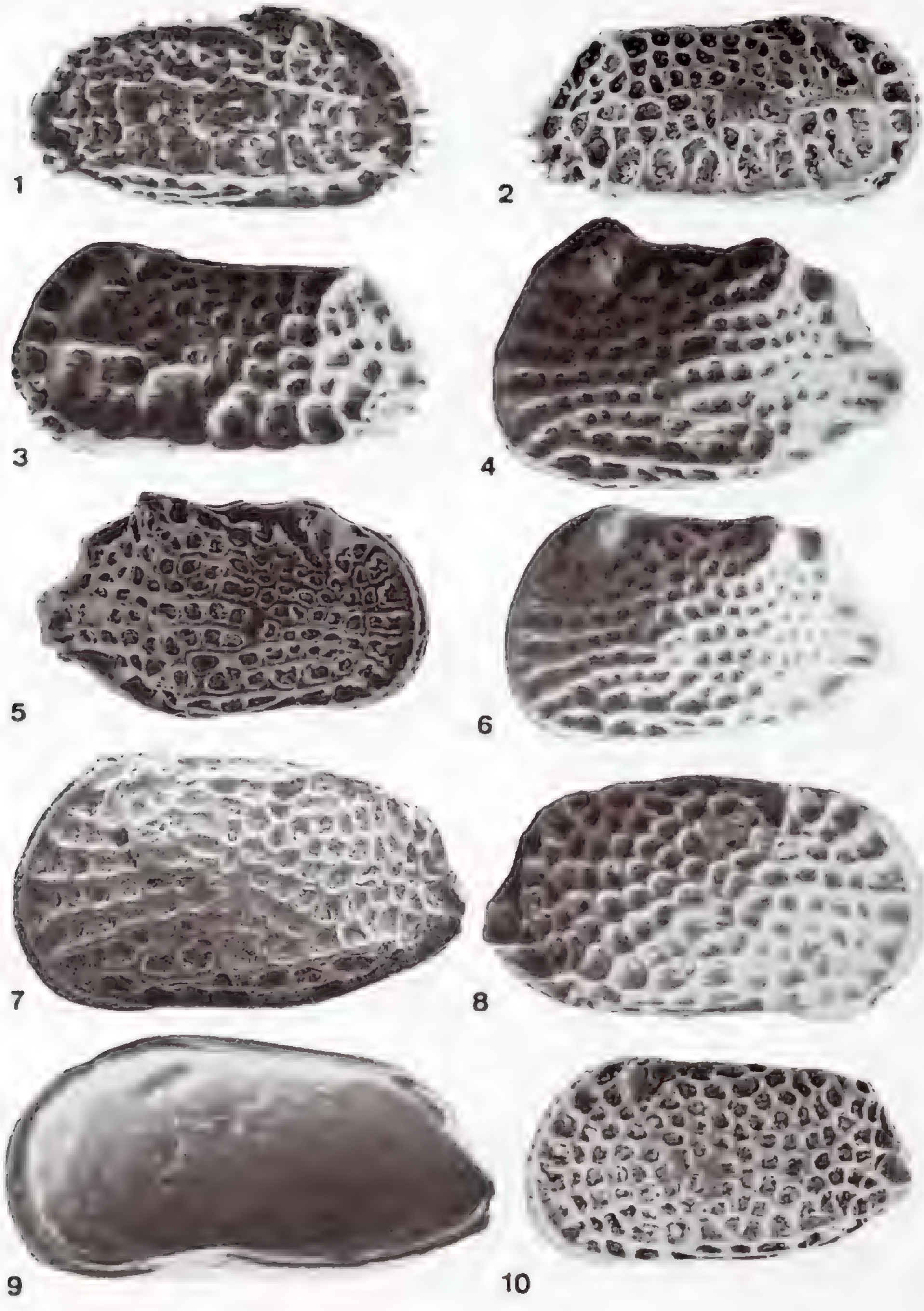

PLATE 9

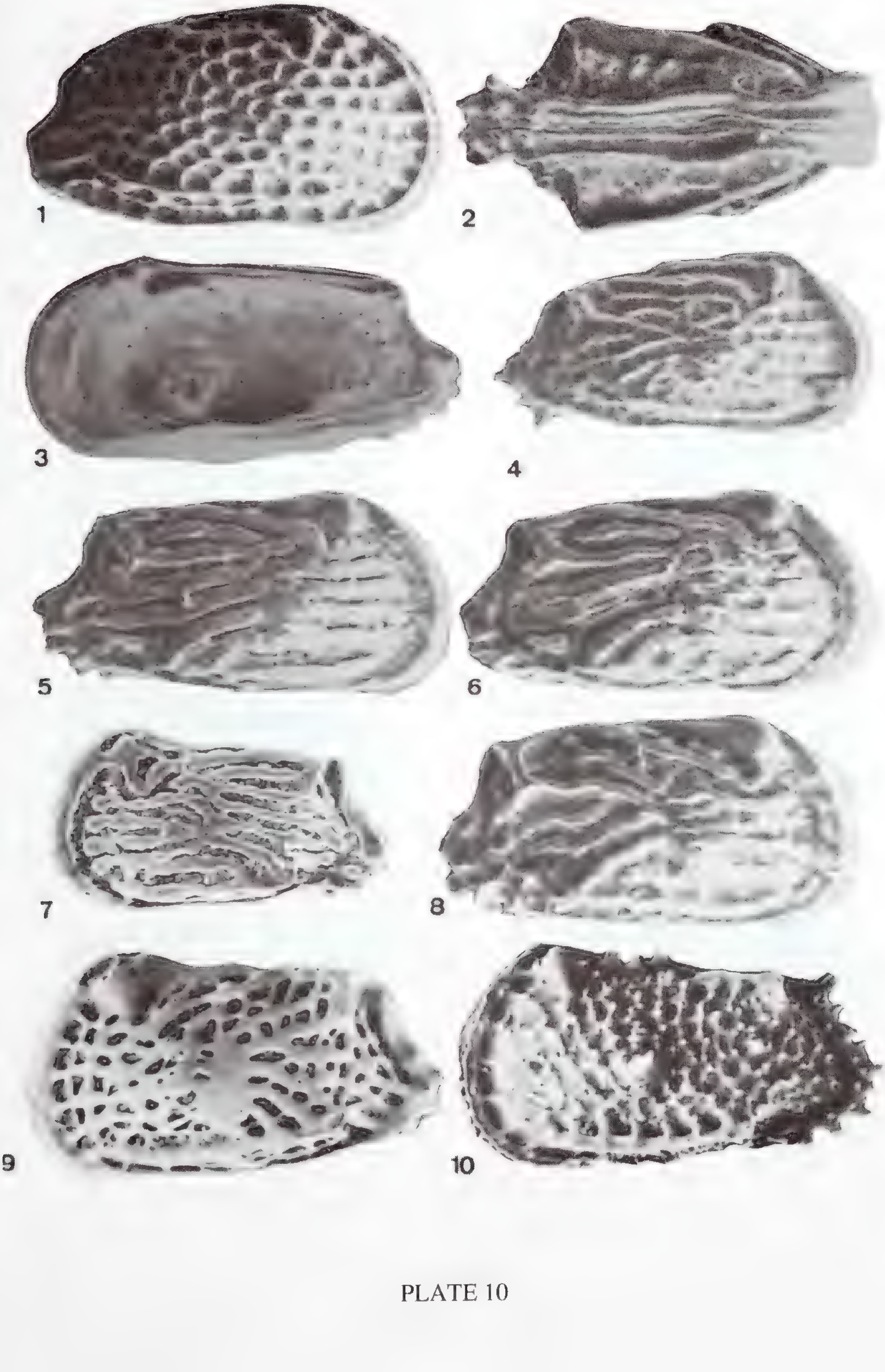

PLATE 10

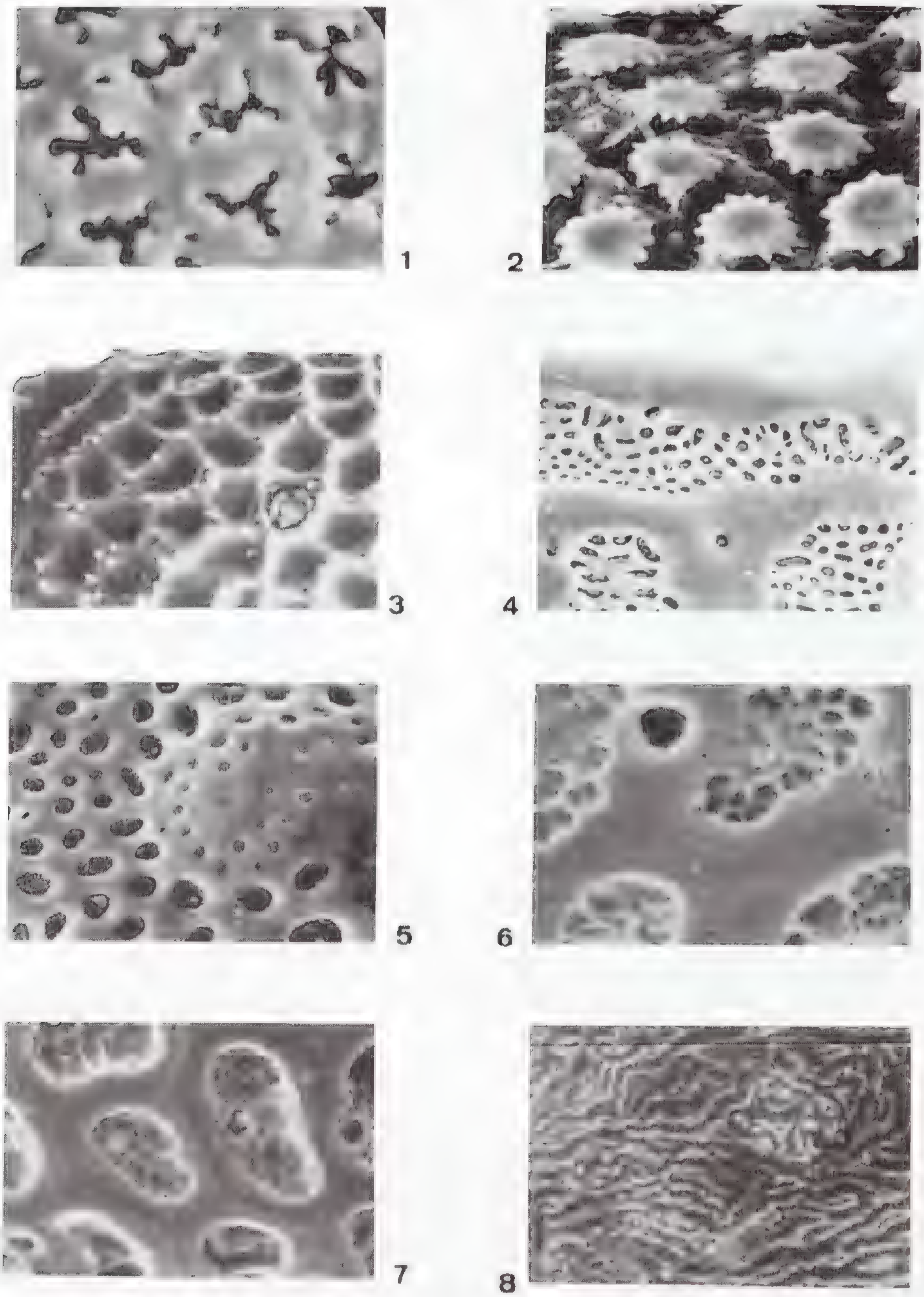

PLATE 11

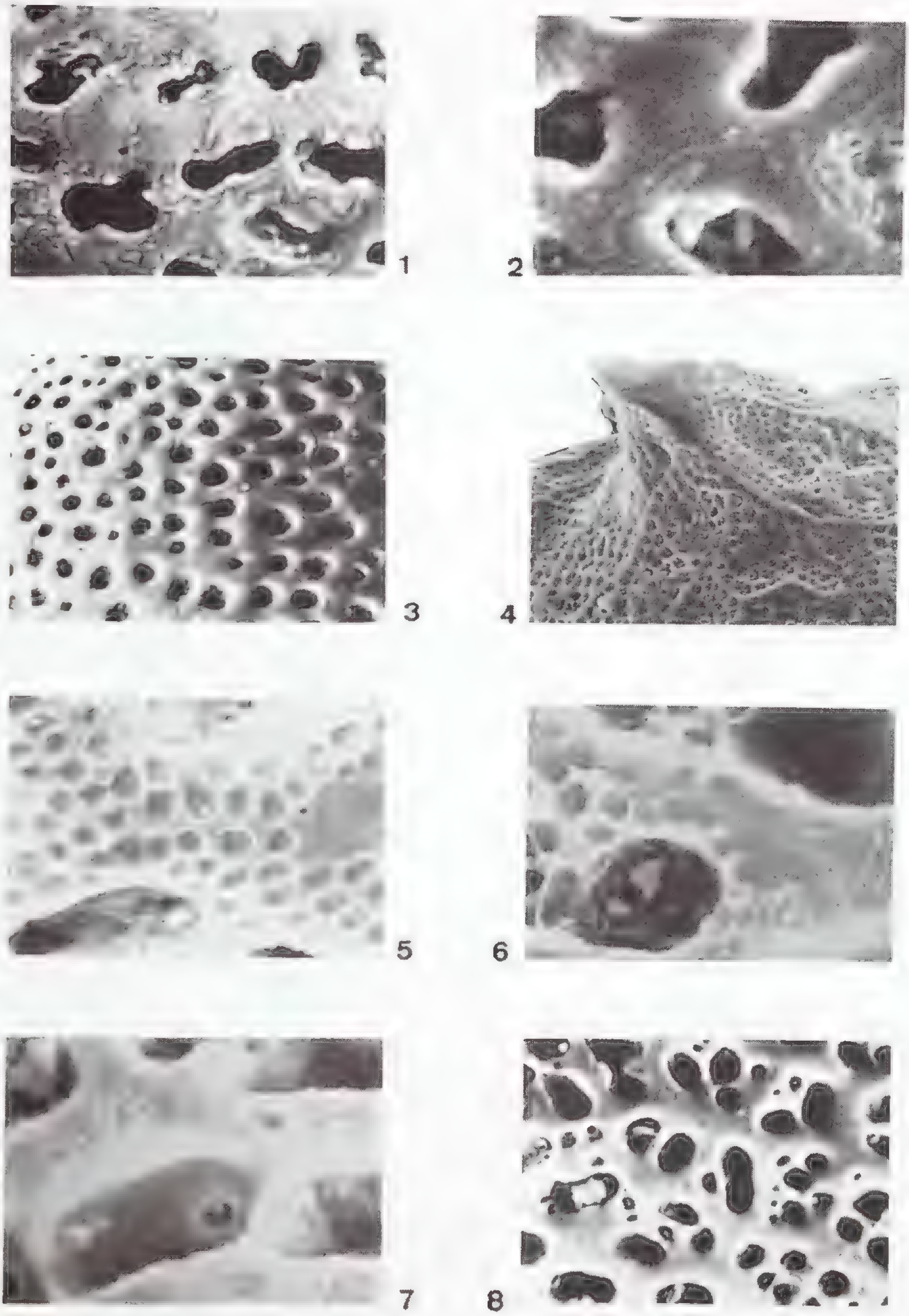

PLATE 12

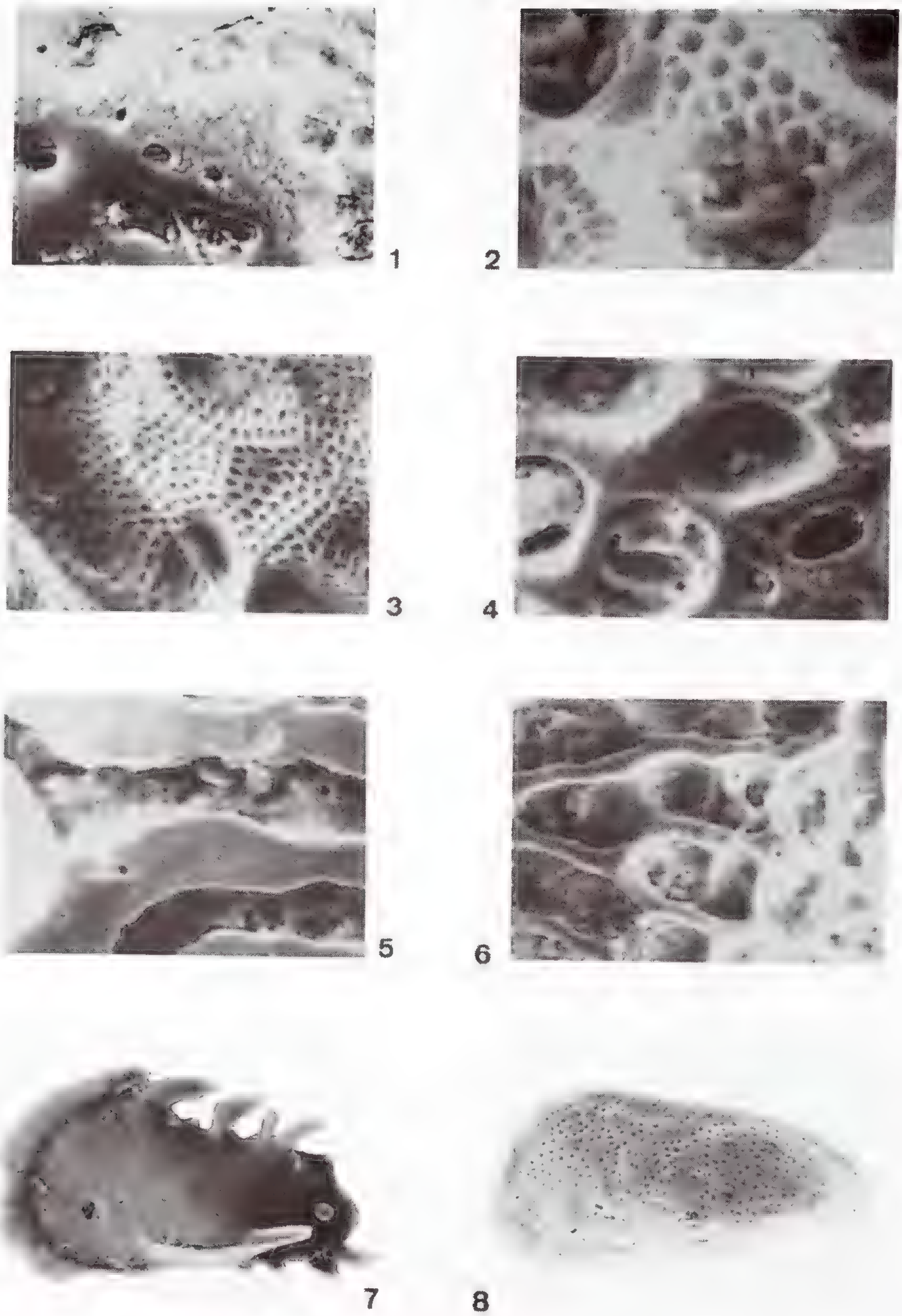

PLATE 13

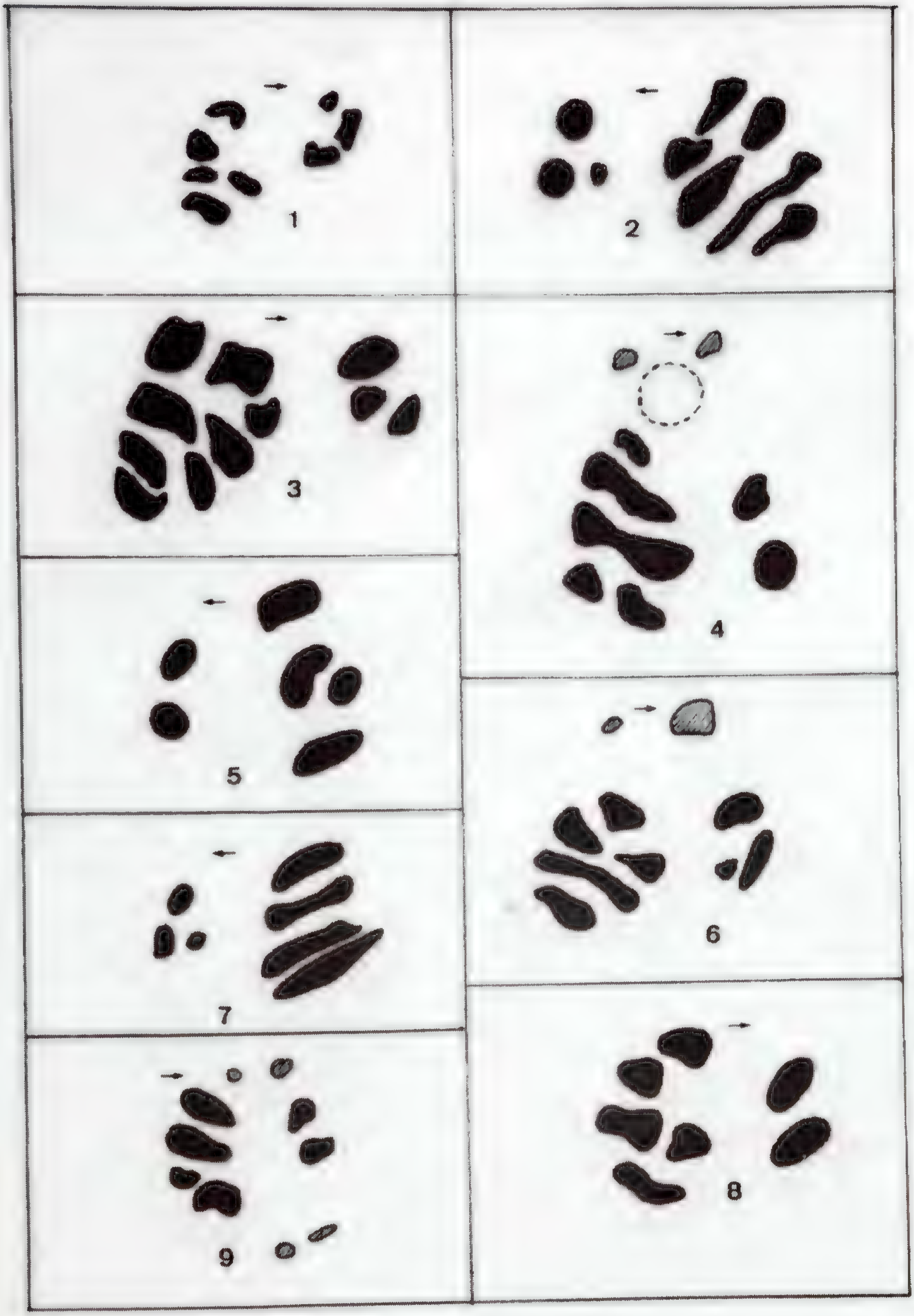

PLATE 14

Memoirs of the Museum of Victoria 54: 51–78 (1994)

SOME CALLIANASSIDAE AND UPOGEBIIDAE FROM AUSTRALIA WITH DESCRIPTION OF FOUR NEW SPECIES (CRUSTACEA: DECAPODA: THALASSINIDEA)

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Abstract

Ngoc-Ho, N., 1994. Some Callianassidae and Upogebiidae from Australia with description of four new species (Crustacea: Decapoda: Thalassinidea). *Memoirs of the Museum of Victoria* 54: 51–78.

New thalassinidean material from Australia has provided five species of Callianassidae and six of Upogebiidae, four new to science: *Callianassa joculatrix* De Man, *C. lewtonae* sp. nov., *C. propinqua* De Man, *C. sibogae* De Man, *Neocallichirus denticulatus* sp. nov., *Gebiacantha ceratophora* (De Man), *G. poorei* sp. nov., *G. priochela* Sakai, *Upogebia anacanthus* sp. nov., *U. giralia* Poore and Griffin, *U. tractabilis* (Hale).

Most of the species are described and figured. The new species are dealt with in detail; variations and other characteristics of the remaining ones are discussed. *Gebiacantha priochela* Sakai is unusual in possession of two types of males.

Introduction

This work gives further information on the thalassinidean fauna of northern Australia synthesised by Poore and Griffin (1979) and by Sakai (1984, 1988, 1993). New material from the collections of the Museum of Victoria, Melbourne and the Queensland Museum, Brisbane has been captured on the North-west shelf and Queensland. Five species of Callianassidae and six of Upogebiidae are identified, four new.

Manning and Felder (1991) were probably right in stating that the genus *Callianassa* 'comprises a heterogenous assemblage of taxa', and analysis of American species led them to conclude 'that the genus *Callianassa* was a composite of numerous genera and that the family Callianassidae as currently defined (see de Saint Laurent, 1973) also was a composite'. They provided a key to subfamilies and American genera of the Callianassidae and seemed regrettably to have limited their consideration almost exclusively to American callianassids. Many Indo-West Pacific species seem not to fit well into the scheme devised by Manning and Felder. As an example, *Callianassa joculatrix* De Man and *C. sibogae* De Man can be differentiated using their diagnosis only on the possession of a minute rostral spine, scarcely an adequate generic character. A reconsideration of the Indo-Pacific Callianassidae will be taken up. For the time being, the nominal genus *Callianassa* is provisionally used as currently defined (e.g. by De Man, 1928 or de Saint Laurent, 1973) but one species is provisionally assigned to *Neocallichirus* Sakai.

A diagnosis of *Gebiacantha* Ngoc-Ho, 1989 is given in English with a key to species.

Morphological characters used in the description of the mandible, epipods and gill structures of the Upogebiidae were figured and discussed by Ngoc-Ho (1981). For drawing, appendages are laid flat between two microslides or coverglasses when needed, but the telson and uropods always are.

The measurements given (in mm) in the descriptions are: carapace length (cl.) measured from tip of the rostrum to posterior border of the carapace, and total length (tl.) measured from tip of the rostrum to posterior border of the telson.

The material examined come from the collections of the Australian Museum, Sydney (AM), Muséum national d'Histoire naturelle, Paris (MHNH), Museum of Victoria, Melbourne (NMV), Queensland Museum, Brisbane (QM), South Australian Museum, Adelaide (SAMA), Western Australian Museum, Perth (WAM) and Zoologisch Museum, Universiteit van Amsterdam (ZMA).

Callianassidae Dana, 1852

Callianassa Leach, 1814

Callianassa joculatrix De Man

Callianassa joculatrix De Man, 1905 : 610. — Poore and Griffin, 1979: 266, fig. 28. — Sakai, 1988: 53 (key). — Ngoc-Ho, 1991: 287, fig. 3.

Callianassa (Cheramus) joculatrix. — De Man, 1928: 26, 98, 130–137, figs 19, 19a–m (nec. fig. 19b). — McNeil, 1968: 26.

Material examined. Lectotype (selected by Ngoc-Ho, 1991): Indonesia: Labuan Tring Bay (8°44.5'S, 116°2.5'E), 18–27 m, mud, corals, coral sand, ZMA De 102.444 (female, tl. 14.5 mm)

Paralectotypes: ZMA De 102.444 (1 male, 8 females).

Other material. Queensland, NE of Townsville (19°3'S, 146°52'E), 23 m, muddy sand, dredge, G. C. B. Poore and H. Lew Ton on RV *The Harry Messel*, 24 Nov 1982 (stn AIMS 1), NMV J 22656 (31 males, cl. 2–3.5 mm, tl. 6–11 mm and 19 females (5 ovig.), cl. 2–3.5 mm, tl. 6.5–11.5 mm); (18°56'S, 146°50'E), 24 m, (stn AIMS 2), NMV J 22657 (3 males, cl. 2.5–3 mm, tl. 7.5–10 mm and 4 females (1 ovig.), cl. 2.5–3 mm, tl. 7.5–10 mm). Pandora Reef (18°49'S, 146°26'E), deep leeward slope, 12 m, sediment cover, epifauna scarce, M. Riddle, corer, Jul 1985, NMV J 22676 (1 juv. cl. 1.5 mm, 3 females, cl. 3–4 mm, tl. 9–12 mm); Oct 1985, NMV J 22677 (1 female, cl. 2.5 mm, tl. 7.5 mm), NMV J 22678 (2 females, cl. 2–3 mm, tl. 7–8 mm); Feb 1986, NMV J 22679 (3 juv., cl. 1.5–2 mm, 1 female, cl. 3.5 mm, tl. 8 mm); NMV J 22680 (5 juv., cl. 1–2 mm); transition between coral and sediment, NMV J 22681 (4 juv., cl. 1–1.5 mm, 1 female, cl. 2 mm, tl. 6 mm); Jul 1985, 10 m, NMV J 22682 (1 juv., cl 1.5 mm, 1 male, cl. 3 mm, tl. 8.5 mm); reef flat, coral rubble, 1 m, NMV J 22683 (1 male, cl. 2 mm, tl. 5.5 mm, 1 female, cl. 2.5 mm, tl. 8.5 mm)

Distribution. Indonesia, north-west and north-east Australia, New Caledonia (east and south).

Remarks. These specimens are smaller than all those previously recorded with no adults larger than 12 mm in total length. Other material from Queensland reached a total length of 14.5 mm (Poore and Griffin, 1979). A female of 18.3 mm from Indonesia (De Man, 1928) and abundant material from New Caledonia (Ngoc-Ho, 1991), reaching 18.5 mm, are significantly larger.

Callianassa lewtonae sp. nov.

Figure 1

Material examined. 2 ovig. females, tl. 19 mm and 19.5 mm

Holotype. Queensland, Britomart Reef, reef front (18°17'S, 146°38'E), 15 m, crinoids, G. C. B. Poore and H. Lew Ton on RV *The Harry Messel*, 27 Nov 1982, SCUBA (stn AIMS 57), NMV J 22659 (ovig. female, cl. 5 mm, tl. 19.5 mm)

Paratypes. Queensland. NE of Townsville (18°43'S, 146°45'E), 34 m, muddy sand, dredge, G. C. B. Poore and H Lew Ton on *The Harry Messel*, 24 Nov 1982 (stn AIMS 4), MNHN-Th 1247 (1 ovig. female, cl. 5 mm, tl. 19 mm) Pandora Reef (18°49'S, 146°26'E), reef flat, 1 m, coral rubble, M. Riddle, corer, May 1986, NMV J22684 (1 female, cl. 4.5 mm, tl. 16 mm).

Description. Rostrum longer in holotype than in paratype, approximately triangular with acute tip, about half length of eye-stalks; cornea elongated laterally, well pigmented.

Antennule with first peduncular article slightly longer than second, third article 3 times longer. Antennal peduncle nearly as long as antennular, terminal article about half length of penultimate. Maxilliped 1: endopod rounded, very small, epipod large with truncate anterior lobe. Maxilliped 3: ischium-merus combined about 1.5 as long as broad; ischium twice as long as merus with row of about 12 spinules on mesial surface; merus unarmed, twice as broad as long, inner lateral and distal borders fused, strongly lobed.

Chelipeds both of same morphology and nearly same size: ischium with 5–6 ventral spinules; merus as long as ischium, unarmed (or with median ventral spinule in paratype (NMV J22684); carpus subtriangular, unarmed, comparatively more slender in left and smaller cheliped than in right; palm slightly longer than fixed finger, latter with 5 denticles on cutting edge; dactylus slender, weakly incurved.

Pereopod 3: carpus triangular, propodus with moderate rounded posterior lobe and small longitudinal carina on external surface.

Telson about as long as wide, greatest width at proximal third, posterolateral angles rounded, posterior margin nearly straight.

Uropod: both endopod and exopod slightly longer than telson; endopod with lateral margins nearly parallel and posterior margin rounded; broadened posterior margin of exopod with small dorsal setose lobe.

Etymology. The species is named for Helen Lew Ton, Museum of Victoria, who collected the material.

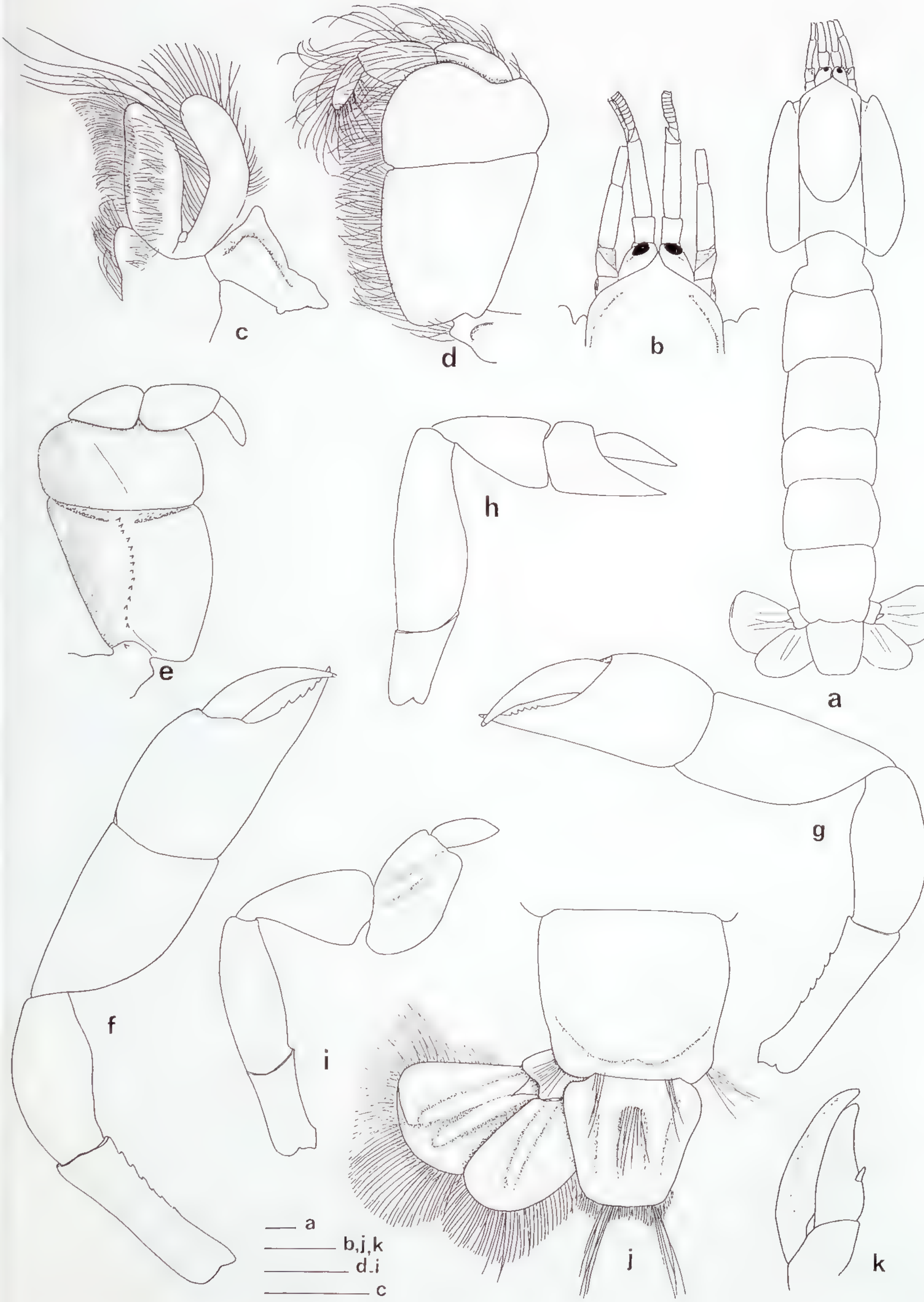
Remarks. This new taxon is similar to *Callianassa amboinensis* De Man, 1888 in the shape of the eyes, maxilliped 3, telson and uropods. It can be differentiated from it by:

1, the antennular and antennal peduncles are

Figure 1. *Callianassa lewtonae* sp. nov. Holotype, ovig. female, tl. 19.5 mm (NMV J22659): b, f–k. Paratype, ovig. female, tl. 19 mm (MNHN-Th 1247): a, c–e

a, body in dorsal view, b, anterior part of carapace, c, maxilliped 1, d, maxilliped 3, external view, e, same, mesial view, f and g, right and left cheliped 1, h, cheliped 2, i, pereopod 3, j, telson and left uropod, k, pleopod 3

Scale lines: 1 mm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of about the same length (antennular peduncle longer in *C. amboinensis*);

2, the operculiform "ischium-merus combined" of the third maxilliped is more than 1.5 times as long as broad (1.2 times in *amboinensis*);

3, chelipeds are more slender with merus unarmed (bearing spinules on ventral border); its carpus is longer than the palm (about half length of palm); its cutting edge of dactylus is unarmed (denticulated);

4, the propodus of pereopod 3 has a large ventroposterior lobe and a longitudinal carina on external surface.

Species such as *C. lewtonae* with the first pair of chelipeds of about the same size and morphology are rare in the genus *Callianassa*. Nevertheless, it can be noted that the type material of this new species includes only females, and males may not share this perculiarity.

Callianassa propinqua De Man

Figure 2

Callianassa propinqua De Man, 1905: 609. — Ngoc-Ho, 1991: 290, fig. 4.

Callianassa (*Cheramus*) *propinqua*. — De Man, 1928b: 127, figs 18–18d.

Material examined. Western Australia, North-west Shelf, between Port Hedland and Dampier (18°41'S, 118°39'E), 134 m, muddy sand, WHOI epibenthic sled, G. C. B. Poore and H. M. Lew Ton on RV *Soela*, 4 Jun 1983 (stn NWA 21), MNHN-Th 1254 (1 male, cl. 3.5 mm, tl. 14 mm and 1 female, cl. 4 mm,tl. 15 mm); (18°50'S, 117°39'E), 178 m, shelly sand, 6 Jun 1983 (stn NWA 29), NMV J22660 (1 male, cl. 2 mm, tl. 7.5 mm and 1 ovig. female, cl. 3 mm, tl. 10.5 mm); (19°5'S, 117°26'E), 120 m, muddy sand, 12 Jun 1983 (stn NWA 52), NMV J22661 (2 male, cl. 3–3.5 mm, tl. 10.5–12.5 mm).

Supplementary description. Antennal peduncle overeaching antennular peduncle for about half of last article.

Large cheliped slightly stouter in males than in females. Ischium and merus with 6–8 ventral spines and 0–6 ventral spinules respectively. Fixed finger and dactylus unarmed, tip slightly curved in males. Small cheliped: ischium and merus with 4–5 and 0–2 ventral spinules respectively.

Pleopod 1 uniramous and pleopod 2 biramous, of about the same size in males as in females, absent in male of tl. 7.5 mm.

Telson approximately two-thirds as long as sixth abdominal segment and a little longer than broad; posterolateral angles rounded, with 2 spinules on each side; posterior border weakly convex, slightly wider in males than in females, with median spinule.

Uropod: endopod linguiform, about as long as telson; exopod almost 1.5 times longer, subrectangular, setose dorsal lobe small, near upper part of posterior border.

Distribution. Indonesia (Kwandang Bay), New Caledonia, Australia (North-west Shelf).

Remarks. This material agrees with the holotype examined previously, a female of tl. 13 mm, and also with the male specimen (MNHN-Th 1201) from New Caledonia (see Ngoc-Ho, 1991). At the same time, it provides the first female large cheliped, missing in the holotype. In males and females, the spination of the meral ventral border of this cheliped varies and smaller specimens carry fewer spinules.

De Man (1928) considered *Callianassa propinqua* as closely related to *C. praedatrix* De Man, 1905 whose holotype is examined and figured (fig. 2a). This specimen, lacking the small first cheliped, is not a female as De Man stated (1928), but a male of tl. 23 mm, with gonopores on the fifth coxae and rudimentary pleopods (figs 2b, 2c).

The male large cheliped of *Callianassa propinqua* and *C. praedatrix* (see De Man, 1928, fig. 22c; Ngoc-Ho 1991, fig. 4g) are very similar as are the carapace and abdomen. The two can still be differentiated by the maxilliped 3, the telson and uropods; maxillipeds 3 of both are similar in having a median spine on the distal border of the ischium (De Man, 1928, fig. 22b; Ngoc-Ho 1991, fig. 4d), but the ischium and merus are more expanded laterally in *C. praedatrix*. Also, the sixth abdominal segment is shorter in *C. praedatrix* than in *C. propinqua*, measuring less than 1.5 times the length of the telson. Likewise, the uropod in *C. praedatrix* is comparatively stouter and shorter (fig. 2a) than in *C. propinqua* (fig. 2f).

Callianassa sibogae De Man

Figure 3

Callianassa Sibogae De Man, 1905: 613.

Callianassa (?*Cheramus*) *Sibogae*. — De Man, 1928: 124, fig. 17–17e.

Material examined. Holotype. Indonesia (7°46'S, 114°30'E), Siboga Expedition, 330 m, bottom mud, ZMA De 102.439 (male, cl. 6.8 mm, tl. 22.8 mm, without P1, P3, P4).

Western Australia. North-west Shelf, between Port Hedland and Dampier (18°41'S, 118°39'E), 134 m, muddy sand, WHOI epibenthic sled, G. C. B. Poore and H. M. Lew Ton RV *Soela*, 4 Jun 1983 (stn NWA 21), NMV J22662 (1 male, cl. 4 mm, tl. 13 mm; 1 female, cl. 5.5 mm, tl. 18 mm); (18°45'S, 118°24'E), 142 m, trawl, 5 Jun 1983 (stn NWA 23), MNHN-Th 1248 (1 female, cl. 4 mm, tl. 13 mm).

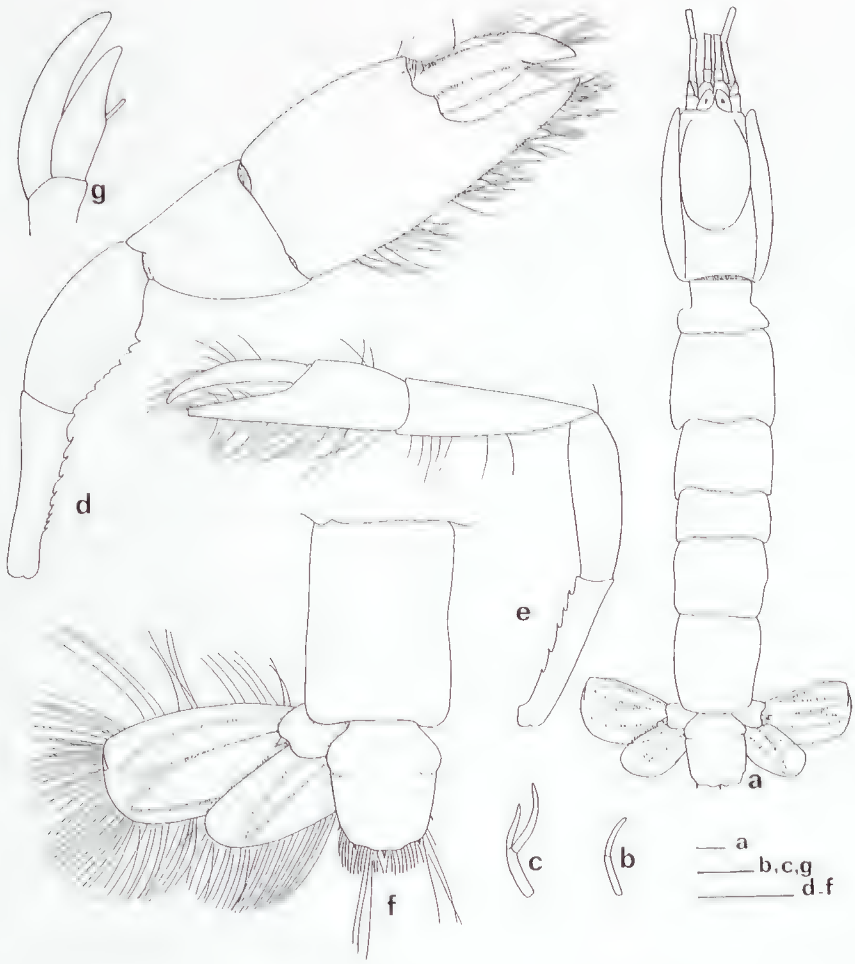


Figure 2. *Callianassa praedatrix* De Man. Holotype, male, tl. 23 mm (ZMA-De 102 433): a, body in dorsal view; b, pleopod 1; c, pleopod 2.

Callianassa propinqua De Man. Female, tl. 15 mm (MNHN-Th 1254): d, large cheliped 1; e, small cheliped 1; f, telson and left uropod; g, pleopod 3.

Scale lines: 1 mm.

Description. Carapace with rostrum pointed anteriorly, a little compressed laterally, as long as eye stalks. Second abdominal segment (fig. 3a) broader than long, with terga expanded laterally into narrow longitudinal strip on each side. Third and fourth abdominal segments broader than long, lateral tergal expansion less conspicuous.

Antennal peduncle overreaching antennular peduncle by its last article.

Maxilliped 3: ischium nearly twice as long as broad and twice as long as merus with longitudinal row of about 22 spinules near outer lateral margin of mesial surface. Merus longer than broad, inner lateral margin slightly convex, distal margin oblique, slightly curved.

Female large cheliped: ischium with 5 ventral spinules. Merus with small proximal spine and larger one near middle of ventral margin. Carpus triangular, about as long as merus. Palm almost 1.5 times as long as fixed finger and dactylus, both fingers of same length, slender, unarmed, with slightly incurved tip. Female small cheliped: ischium and merus of nearly same length, ischium with 5 ventral spinules, merus with 1 spine near middle of ventral margin; carpus over 3 times as long as broad; palm shorter than slender fixed finger and dactylus, latter slightly curved.

Pereopod 3: propodus slender, not expanded ventrally.

Pleopod 1 uniramous, pleopod 2 biramous, larger in females of tl. 13 mm and 18 mm than in male holotype of 22.8 mm, absent in male of tl. 13 mm.

Telson longer than broad, posterolateral angles rounded, each with 2 minute spinules often broken off, posterior margin with median spinule.

Uropod: endopod somewhat triangular, about as long as telson; exopod with rounded posterior border and small dorsal setose lobe, longer than telson, up to about 1.5 times longer in specimen of tl. 18 mm.

Distribution. Indonesia, Australia (North-west Shelf).

Remarks. Besides providing the morphology of the female first chelipeds, the material studied confirms De Man's view of the species' distinguishing characters. They are: laterally compressed acuminate rostrum, laterally expanded abdominal terga especially on the second segment, maxilliped 3 with a relatively narrow ischium-merus, telson longer than broad, and uropods longer than the telson with exopod of an ovoid shape. Among these features, the first two are likely to be the most reliable. As for the uropods, the exopod is longer and more slender in larger specimens.

From the material studied, in females, both first chelipeds bear spinules on the ventral border of the ischium and a median spine on the same border of the merus. Other articles are unarmed; the fixed finger and dactylus are slender, with incurved tip.

Neocallichirus Sakai, 1988

Neocallichirus denticulatus sp. nov.

Figure 4

Material examined. 2 females, tl. 19 mm and 20.5 mm.
Holotype. Queensland NE of Townsville (18°56'S, 146°50'E), 24 m, muddy sand, dredge, G. C. B. Poore and H. Lew Ton on RV *The Harry Messel*, 24 Nov 1982 (stn AIMS 2), NMV J22658 (female, cl. 6.5 mm, tl. 20.5 mm).

Paratype. Queensland (18°50'S, 146°47'E), 26 m (stn AIMS 3), MNHN-Th 1246 (1 female, cl. 5.5 mm, tl. 19 mm).

Description. Carapace produced anteriorly into triangular downturned rostrum and spine on each side, posterior to eye. Eye-stalks slightly shorter than first segment of antennular peduncle, with obtuse mesiodistal tip; cornea well pigmented, convex, subterminal.

Abdomen with second and sixth segments the largest, sixth slightly larger.

Antennular peduncle with last segment twice as long as penultimate. Antennal peduncle exceeding antennular by half of its last segment, latter about two-thirds length of penultimate.

Maxilliped 1: endopod small and rounded; epipod large, anterior lobe elongated with pointed tip.

Maxilliped 2: with small epipod.

Maxilliped 3: ischium-merus combined as moderately broad plate; ischium over twice as long as merus with curved row of about 17 spinules on mesial surface; merus unarmed, inner lateral margin curved; carpus broadened distally; propodus about as long as wide with rounded lower margin; dactylus slender, about as long as propodus and one-fourth as broad.

Large cheliped: ischium and merus of approximately same length, with 10 and 8 spinules respectively; carpus about half length of palm, unarmed; palm with lower margin denticulated throughout in specimen of tl. 20.5 mm, with few proximal denticles in specimen of tl. 19 mm; fixed finger and dactylus about half length of palm, both with incurved tip, fixed finger with serrated cutting edge, same border of dactylus with denticles and 1 or 2 larger triangular teeth.

Small cheliped: ischium slightly shorter than

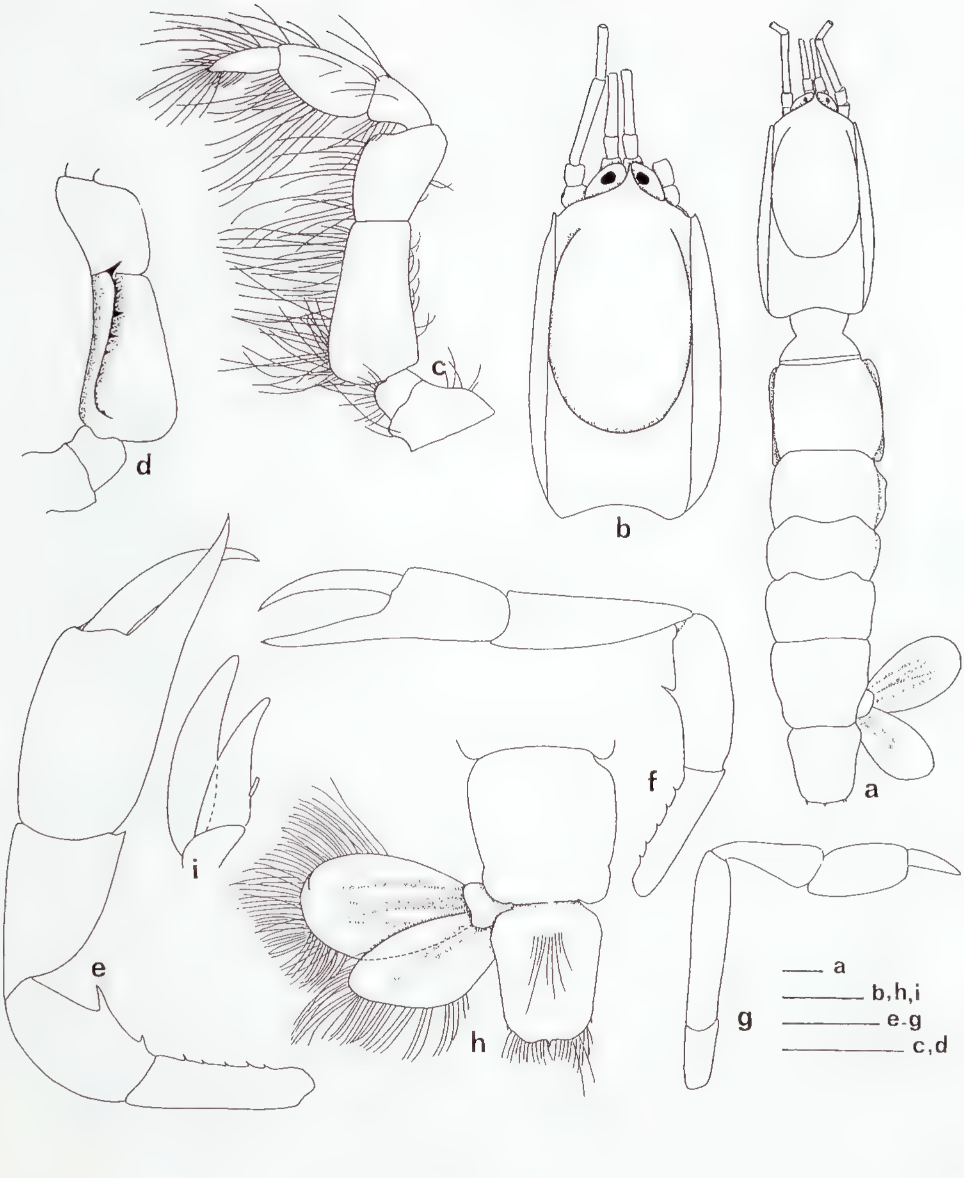
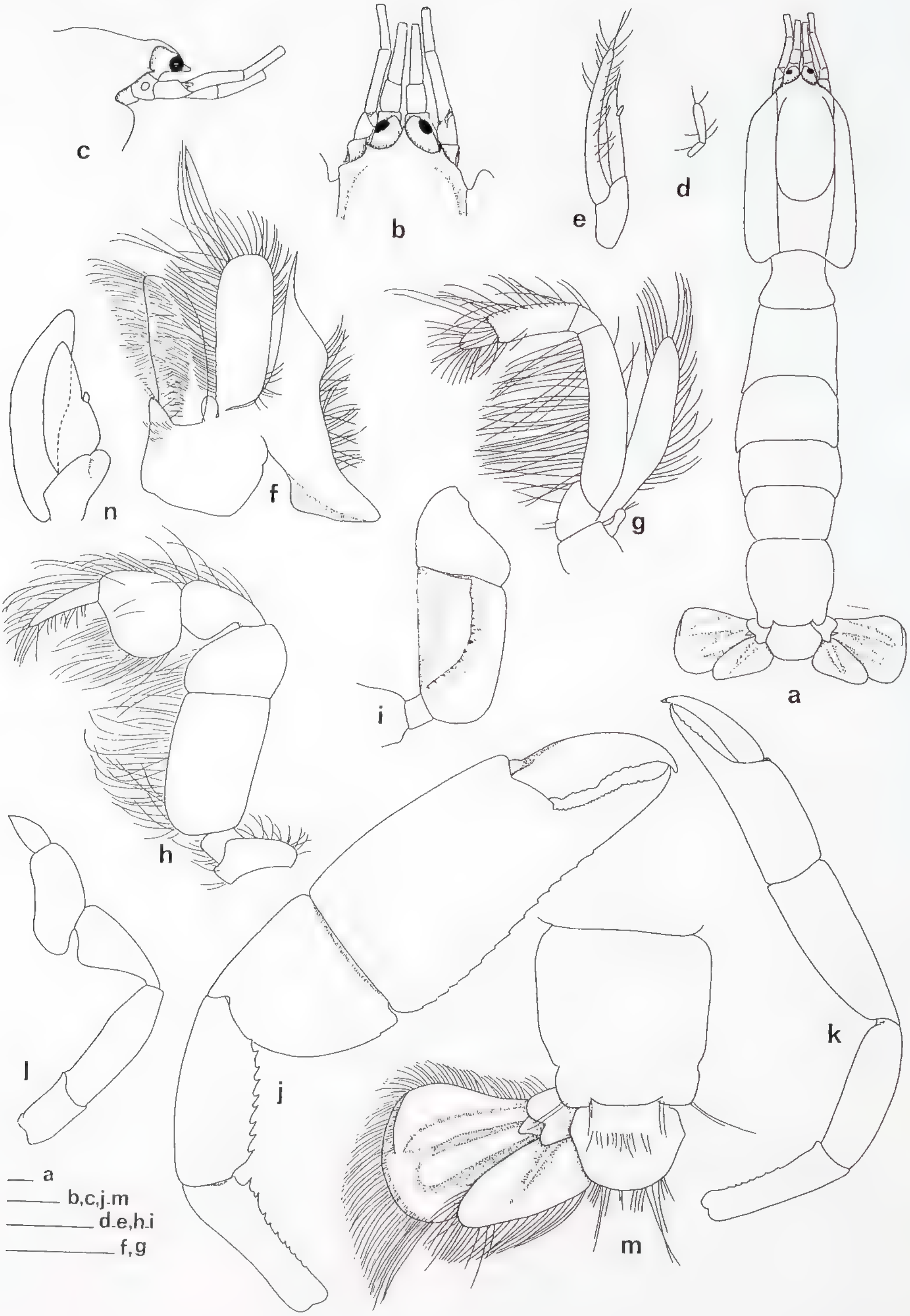


Figure 3. *Callianassa sibogae* De Man. Female, tl. 18 mm (NMV J22662): a, c, d, i. Female, tl. 13 mm (MNHN-Th 1248): b, e–h.

a, body in dorsal view; b, carapace, dorsal view; c, maxilliped 3, external view; d, same, basis, ischium and merus, mesial view; e, large cheliped 1; f, small cheliped 1; g, pereopod 3; h, telson and left uropod; i, pleopod 3.

Scale lines: 1 mm.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merus with 7–8 lower denticles; carpus 1.5 times as long as palm, both unarmed; fixed finger and dactylus about as long as palm, both with incurved tip, cutting edge of fixed finger bearing 3–4 denticles.

Pereopod 3: propodus with ventroposterior lobe not exceeding lower margin of carpus.

Female pleopod 1 small, uniramous.

Female pleopod 2 biramous, endopod shorter bearing small appendix interna.

Telson about half length of sixth abdominal segment and as long as wide, widest at proximal third, tapering posteriorly to weakly convex posterior margin.

Uropod: endopod lanceolate, widest proximally and about 1.5 times length of telson; exopod longer than endopod, twice as long as telson, posterior margin broadened, dorsal setose lobe large.

Distribution. Australia (north Queensland).

Remarks. This new taxon resembles species of the genus *Corallianassa* Manning, 1991 in posessing a trispinous frontal margin, in the morphology of maxilliped 3 and of the uropods that are longer than the telson. Nevertheless, while the frontal margin is strongly spinous in Manning's genus, anterior spines are small in *N. denticulatus* and the rostrum is downturned. Furthermore, the palm of its larger pereopod 1 bears ventral denticles whilst it is unarmed in *Corallianassa*.

According to Manning and Fielder's key (1991) and its appendages, the present species is more closely related to *Neocallichirus* Sakai where it is provisionally placed. It differs from the diagnosis of *Neocallichirus* (Sakai, 1988; Manning and Fielder, 1991) by its rounded eyes (dish-shaped in typical *Neocallichirus)* and the slender uropod endopod, longer than the telson.

Neocallichirus denticutatus can be differentiated from other Australian species of *Neocallichirus*, *N. horneri* Sakai, 1988, *N. caechabitator*, Sakai, 1988, *N. darwinensis* Sakai, 1988 and *N. limosa* (Poore, 1979) by:

1, trispinous frontal margin;

2, uropod endopod more slender and longer than telson; and

3, except for *N. darwinensis*, uropod exopod proportionally much longer and nearly twice as long as telson.

The weakly trispinous frontal margin, the ventral denticulation of pereopod 1 palm, the length of the uropods bring this species near to the American *N. rathbunae* (Schmitt, 1935). The two differ in the following features:

1, rostral spine downturned in *N. denticulatus* (straight in *N. rathbunae*);

2, rounded eyes (dish-shaped);

3, ventral border of pereopod 1 carpus unarmed (denticulated); and

4, uropod endopod oblong, slender (nearly quadrate).

Upogebiidae Borradaile, 1903

Gebiacantha Ngoc-Ho, 1989

Diagnosis. One or many infrarostral spines. Anterolateral border of carapace with 2 or more spinules. Posterior border of telson more or less concave. Mandible without acute anterior tooth. Maxilliped 1 without epipod, maxilliped 3 with small epipod or (rarely) without, mesial surface of ischium with longitudinal row of fine spinules representing vestigial *crista dentata*. Gill filaments relatively narrow and undivided (making single row on each side of rachis). Pereopod 1 subcheliform, carpus and propodus with numerous spines, fixed finger a spiniform projection, not exceeding half length of dactylus. Coxae of pereopod 1–3 or pereopod 1–4 with mesial spines or spinules. Uropod relatively long, exopod always longer than telson.

Remarks. As stated by Ngoc-Ho (1989) a subdivision of the Upogebiidae is considered very difficult by many authors (De Saint Laurent and Le Loeuff, 1979; Sakai, 1982; Williams, 1986) and requires precise criteria. In *Gebiacantha* the morphology of the rostrum, pereopods, telson and uropods, the mouth appendages and

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Figure 4. *Neocallichirus denticutatus* sp. nov. Holotype, female, tl. 20.5 mm (NMV J22658): a–c, j–n. Female, tl. 19 mm (MNHN-Th 1246): f–i.

a, body in dorsal view; b and c, anterior part of carapace, dorsal and lateral view; d, pleopod 1; e, pleopod 2; f, maxilliped 1; g, maxilliped 2; h, maxilliped 3, external view; i, basis, ischium and merus of same, mesial view; j, large cheliped 1; k, small cheliped 1; l, pereopod 3; m, telson and left uropod; n, pleopod 3.

Scale lines: 1 mm.

branchial filaments are taken into account. These are homogeneous in the family and any variation should be of evolutionary significance. The genus is defined by the combination of characters listed in the diagnosis.

Fifteen species of *Gebiacantha* have now been described: *G. talismani* (Bouvier, 1915, type species), *G. ceratophora* (De Man, 1905), *G. monoceros* (De Man, 1905), *G. acanthochela* (Sakai, 1967), *G. acutispina* (de Saint Laurent and Ngoc-Ho, 1979 of which *G. niugini* Poore, 1982 is a junior synonym), *G. plantae* (Sakai, 1982), *G. arabica* Ngoc-Ho, 1989, *G. lagonensis* Ngoc-Ho, 1989, *G. laurentae* Ngoc-Ho, 1989, *G. reunionensis* Ngoc-Ho, 1989, *G. richeri* Ngoc-Ho, 1989, *G. poorei* sp. nov., *G. priochela* Sakai, 1993, *G. lifuensis* Ngoc-Ho, 1994 (?), *G. multispinosa* Ngoc-Ho, 1994 (?).

Table 1. Distinguishing characters between *Gebiacantha priochela* and *G. plantae*.

	G. priochela		*G. plantae*	
Infrarostral spine	2–3		2–4	
Spines on anterolateral border of carapace	5–7		1–3	
Spines on antennal peduncle articles 1, 3 and 4	1, 2–4, 3–4		0, 1, 2–3	
Male pereopod 1	stout type	slender type	stout type	slender type
External tubercles on lower margin of propodus	large	small	small	small
External distal spines between dactylus and fixed finger	1	1	absent	absent
Mesial spines and tubercles	tubercles + spinules	2 rows of spines	tubercles + spinules	3 rows of spines
Ratio of lengths of fixed finger : dactyl	1:10	1:4	1:8	1:4
Dorsal border of dactylus	with quadrate plates		with corneous carina	
Female pereopod 1				
Large carpal subdistal spines	3		3	
Row of mesial spines on propodus	1–2		3	
Dorsal border of dactylus	with tubercles		with tubercles	
External surface of dactylus	few tubercles		tuberculate carina	
Mesial surface of dactylus	small tubercles		tuberculate carina	

Key to species of *Gebiacantha*

1. Exopod of uropod hardly longer than telson, posterior border nearly straight, not continuous with lateral external border; posterior border of telson moderately concave medially 2

— Exopod of uropod at least 1.5 times as long as telson, posterior border rounded, continuous with lateral external border; posterior border of telson strongly concave medially........ 10

2. 5 spinules or more on anterolateral border of carapace 3

— 2–4 spinules on anterolateral border of carapace 8

3. 1–3 infrarostral spines 4

— 3–4 infrarostral spines 5

4. 2 small rostral spines; 4 longitudinal rows of 10–12 spines on mesial surface of propodus of pereopod 1. Japan .... *G. acanthochela*

— 2 large rostral spines; 3 longitudinal rows of 5–8 spines on mesial surface of propodus of pereopod 1. Australia .... *G. poorei*

5. Telson about 1.5 times as broad as long 6
— Telson about as broad as long 7
6. 4 spinules on each lateral shoulder of cervical groove; 6 longitudinal rows of 6–10 spines on mesial surface of pereopod 1 propodus. New Caledonia .... *G. multispinosa*
— 1 spine on each lateral shoulder of cervical groove; 4 longitudinal rows of 3–8 spines on mesial surface of pereopod 1 propodus. New Caledonia .... *G. lifuensis*
7. 1–2 spines on each lateral shoulder of cervical groove; 3 longitudinal rows of 4–8 spines in mesial dorsal part of pereopod 1 propodus; male pereopod 1 not dimorphic. East Atlantic .... *G. talismani*
— 1 spine on each lateral shoulder of cervical groove; 1–3 longitudinal rows of 2–9 spines on mesial surface of pereopod 1 propodus; male pereopod 1 dimorphic with 'stout' and 'slender' types, dactylus of both with transverse dorsal corneous ridges. Australia .... *G. priochela*
8. Pereopod 1 propodus with mesial surface unarmed except for row of dorsal spines (single infrarostral spine). Indo-Pacific .... *G. monoceros*
— Pereopod 1 propodus with numerous spines on mesial surface 9
9. 2–3 large infrarostral spines; male pereopod 1 dimorphic with 'stout' and 'slender' type, both with longitudinal dorsal corneous carina on dactylus; fixed finger less than quarter length of dactylus. Madagascar .... *G. plantae*
— 1–2 small infrarostral spines; male pereopod 1 without longitudinal dorsal corneous carina on dactylus; fixed finger about third length of dactylus, cutting edge denticulated. Gulf of Suez .... *G. arabica*
10. Mesial surface of pereopod 1 propodus not twisted, carpus and prpodus not especially setose 11
— Pereopod 1 propodus twisted, with main part of mesial surface turned upwards; carpus and propodus bearing numerous long setae dorsally 13
11. 1 ventral spine on article 1 of antennular peduncle 12
— 2–3 ventral spines on article 1 of antennular peduncle; 1–3 infrarostral spines; rostrum over 1.5 times as long as broad; spines of moderate size or spinules on mesial surface of pereopod 1 propodus; a large ventral spine behind fixed finger in both sexes. Reunion Island .... *G. reunionensis*
12. 3 infrarostral spines; rostrum approximately triangular and as long as largest breadth; long and sharp spines on mesial surface of pereopod 1 propodus with 2–3 large ventral spines behind fixed finger. North-west Australia, Papua New Guinea .... *G. acutispina*
— 1–2 infrarostral spines; rostrum approximately egg-shaped, about 1.5 times as long as broad; small or large ventral spine on pereopod 1 propodus, behind fixed finger. Indonesia, Queensland (Australia) .... *G. ceratophora*
13. Large teeth on lateral margin of rostrum; proximodorsal part of pereopod 1 propodus not protruding backwards over carpus 14
— Small teeth on lateral margin of rostrum; proximodorsal part of pereopod 1 propodus with prominent backward projection over carpus; mesial surface unarmed between dorsal and ventral row of spines; setae moderately long and dense on carpus and propodus. Indonesia .... *G. laurentae*
14. Mesial surface of pereopod 1 propodus with 2–3 spinules between dorsal and ventral row of spines; long and dense setae on carpus and propodus; single transverse carina on telson. New Caledonia .... *G. lagonensis*
— Mesial surface of pereopod 1 propodus with numerous spines; very long and dense setae on carpus and propodus; double transverse carina on telson. New Caledonia .... *G. richeri*

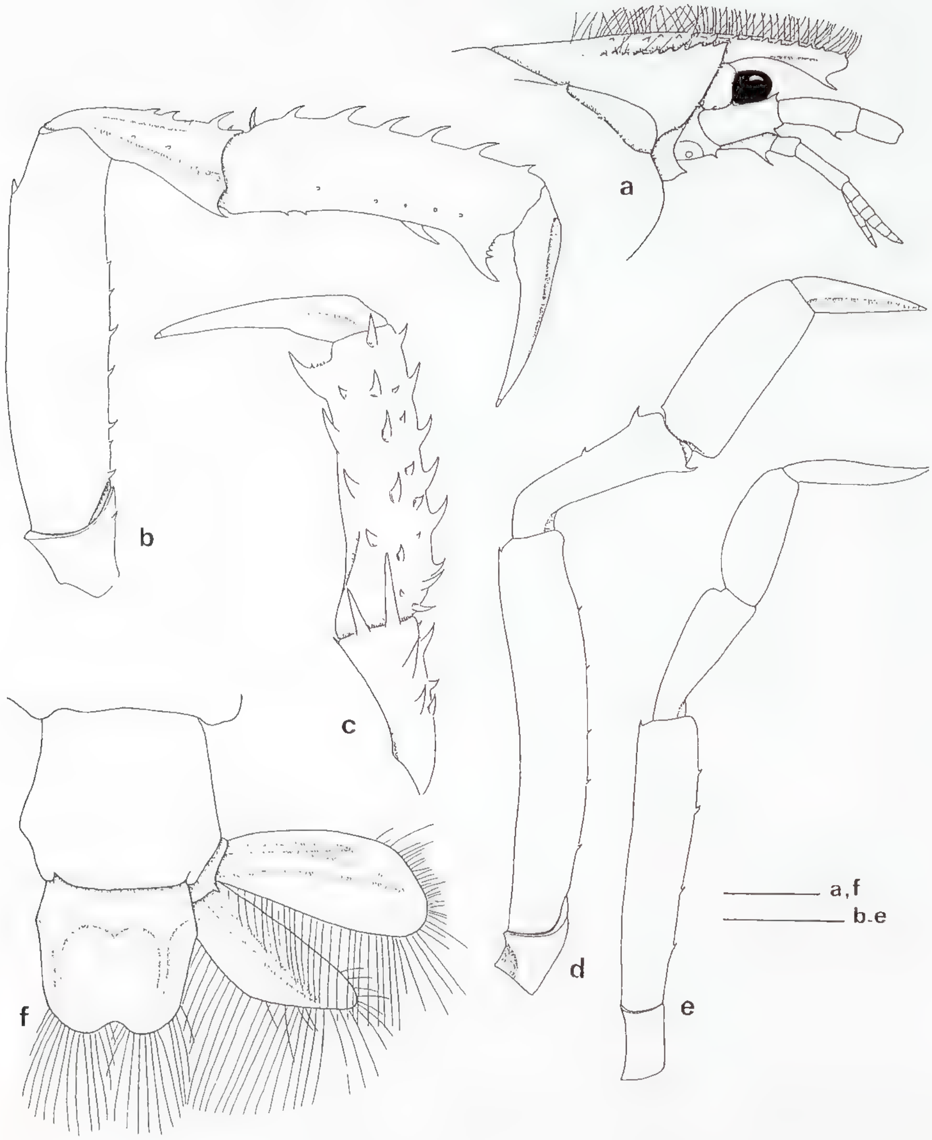


Figure 5. *Gebiacantha ceratophora* De Man. Male, tl. 7.5 mm (NMV J17918): a, anterior part of carapace, lateral view; b, pereopod 1, external view; c, distal articles of pereopod 1, mesial view; d, pereopod 2; e, pereopod 3; f, telson and right uropod.
Scale lines: 0.5 mm.

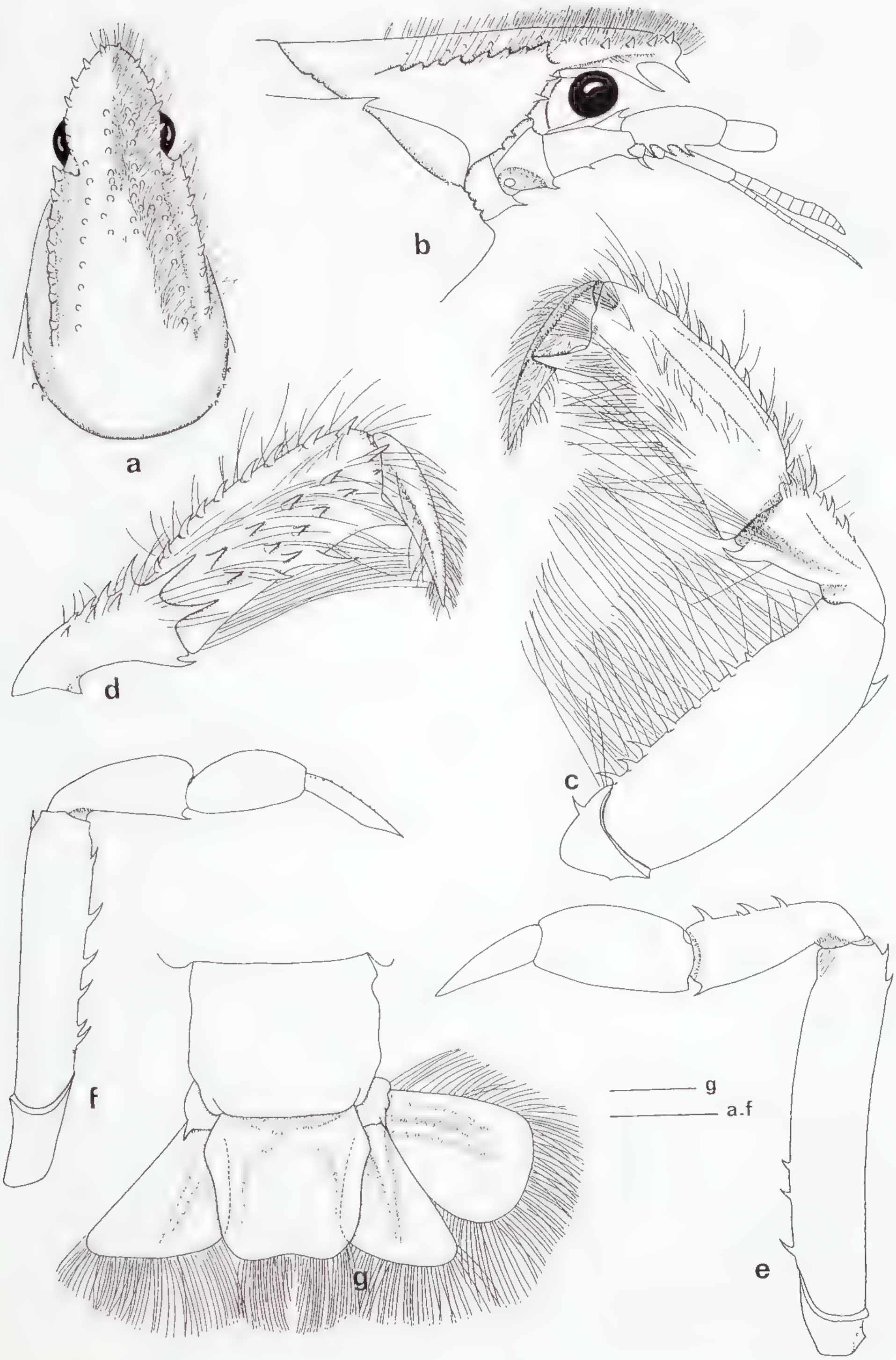


Figure 6. *Gebiacantha poorei* sp. nov. Holotype, male, tl. 14 mm (NMV J17919): a, b, anterior part of carapace, dorsal and lateral view; c, pereopod 1, external view; d, distal articles of same, mesial view; e, pereopod 2; f, pereopod 3; g, telson and uropods.
Scale lines: 1 mm.

Gebiacantha ceratophora (De Man)

Figure 5

Upogebia (*Upogebia*) *ceratophora* De Man, 1905: 602; 1928: 69, figs 9–9g; — Sakai, 1982: 49 (in part), 105.

Upogebia ceratophora .— de Saint Laurent and Ngoc-Ho, 1979: 63, figs 6–8, 22–24.

Gebiacantha ceratophora. — Ngoc-Ho, 1989: 122.

Material examined. Queensland, NE of Townsville (19°3'S, 146°52'E), 23 m, muddy sand, dredge, G. C. B.Poore and H. Lew Ton on RV *The Harry Messel*, 24 Nov 1982 (stn AIMS 1), NMV J17918 (1 male, cl. 3 mm, tl. 7.5 mm); 18°24'S, 146°39'E (stn AIMS 7), NMV J17917 (1 male, cl. 3.5 mm, tl. 8 mm). Pandora Reef, leeward slope (18°49'S, 146°26'E), 10 m, transition between coral and sediment, M. Riddle, corer, Jul 1985, NMV J22686 (1 male, cl. 3.5 mm, tl. 9 mm).

Description. Rostrum approximately 1.5 times as long as broad, projecting far beyond eyes, armed with slender infrarostral spine and another anterior spinule in specimen NMV J22686; 7–8 small teeth dorsally on each lateral border. Lateral ridges of gastric region each with 9–10 spinules; anterolateral border of carapace with 3–4 spinules. Cervical groove moderately deep, shoulder lateral to it bearing 1 spine and 3 spinules on each side.

Antennule: peduncular article 1 with ventral spine; flagella short. Antenna: peduncular article 1, 3 and 4 each with ventral spine; peduncular article 2 with 2 dorsal spinules; scale hardly separated from peduncle, terminating in spinule.

Pereopod 1 slender and subcheliform. Ischium with ventral spine. Merus more than 4 times as long as broad, carrying dorsal subdistal spine, 7–8 spines and spinules on ventral margin. Carpus bearing fine longitudinal groove on upper part of external surface; small ventral and 2 large mesial distal spines; 3 spines and 3 spinules along or near dorsal border. Propodus about 3.5 times as long as broad, 6 dorsal spines and few denticles on proximal third of ventral margin; external surface with few small tubercles in ventral part; mesial surface with 2 longitudinal rows of spines and spinules in dorsal half, lower one terminating in large spine near articulation with dactylus; spinule near base and large ventral spine behind fixed finger, latter spine followed posteriorly by 2 smaller ones; fixed finger small, quarter length of dactylus, cutting edge with denticles proximally. Dactylus bearing corneous tip and fine longitudinal dorsal groove; cutting edge smooth.

Pereopod 2: merus more than 5 times as long as broad with dorsal subdistal and 5 ventral spinules. Carpus bearing spinule near middle of dorsal border, dorsal subdistal and ventral subdistal spines. Dactylus with corneous tip.

Pereopod 3: merus with dorsal distal and 4 ventral spinules. Dactylus lanceolate.

Telson slightly shorter than sixth abdominal segment with faint inverted U-shaped carina on dorsal surface; posterior margin well concave medially.

Uropods: both exopod and endopod slender, longer than telson; protopod with spinule.

Distribution. Indonesia, Australia (Queensland).

Remarks. The new material agrees with the description and figures of De Man (1928) and de Saint Laurent and Ngoc-Ho (1979). These are the first males known and they differ from the types, both females, only in the large mesial spines behind the first pereopod fixed finger. The key to species of *Gebiacantha* has been amended to account for the new characteristics of *G. ceratophora*.

Gebiacantha poorei sp. nov.

Figure 6

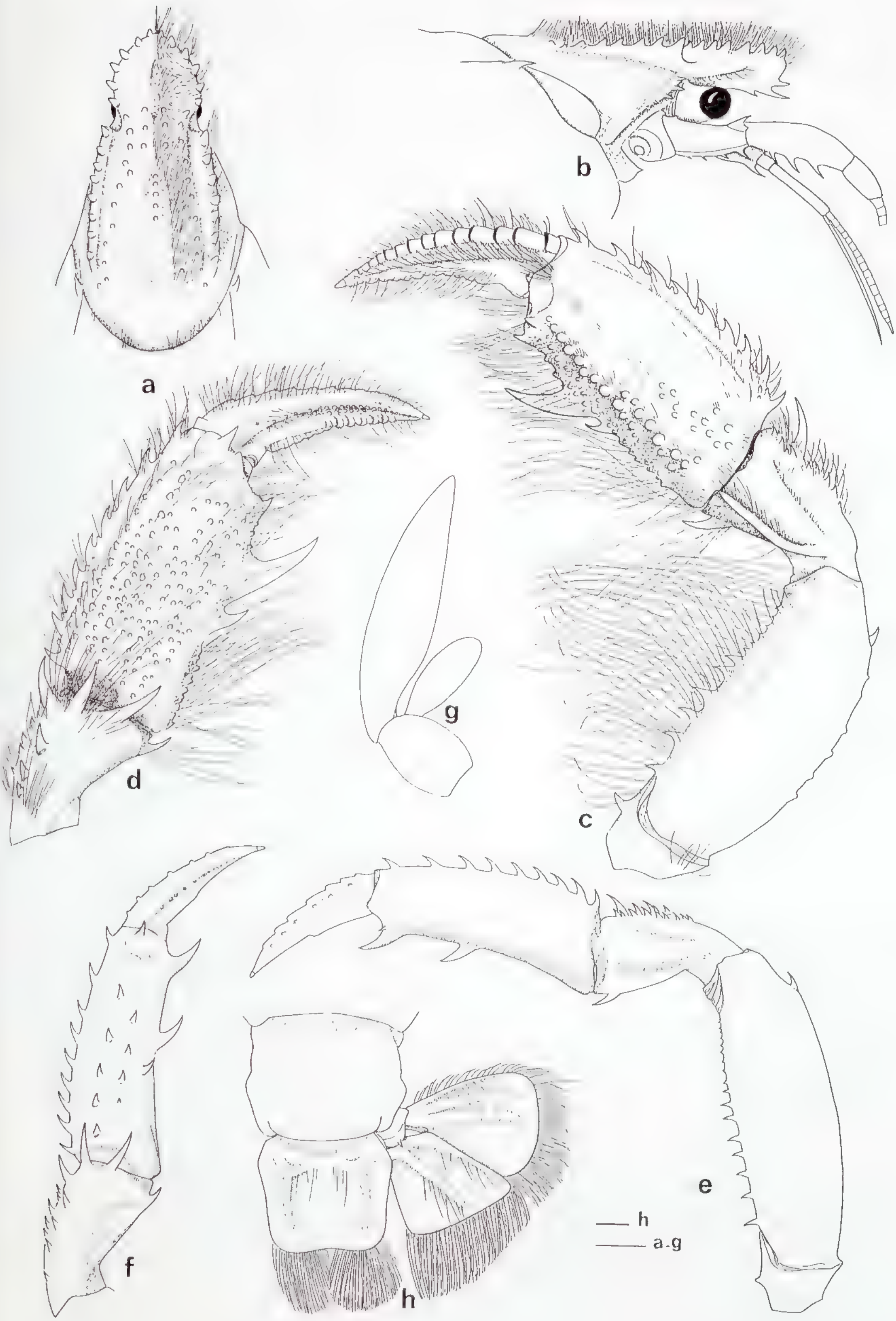
Material examined. Holotype. Queensland, NE of Townsville (18°50'S, 146°47'E), 23 m, muddy sand, dredge, G. C. B. Poore and H. M. Lew Ton on RV *The Harry Messel*, 24 Nov 1982 (stn AIMS 3), NMV J17919 (male, cl. 5.5 mm, tl. 14 mm).

Other material. Type locality, NMV J22667 (male, cl. 2.5 mm, tl. 7 mm); NE of Townsville (18°43'S, 146°45'E), 34 m (stn AIMS 4), NMV J17921 (1 male, cl. 4 mm, tl. 10.5 mm without P1).

Description. Rostrum slightly longer than broad, rounded apically, projecting beyond eyes; dorsal

Figure 7. *Gebiacantha priochela* Sakai. Male, tl. 28 mm (NMV J22663): a–d, g, h; female, tl. 26 mm (NMV J22664): e, f. a, b, anterior part of carapace in dorsal and lateral view; c and e, pereopod 1, external view; d and f, distal part of same, mesial view; g, pleopod 2; h, telson and right uropod.

Scale lines: 1 mm.


a
b
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a-g

surface with fine longitudinal median groove bordered with rounded tubercles and 6–7 spiniform teeth on each lateral border; 2 large ventral spines. Gastric region with most tubercles alongside lateral grooves; lateral ridges with 8 spiniform teeth. Cervical groove deep bearing large spine and 2–3 denticles on each side near intersection with linea thalassinica. Anterolateral border of carapace with 5 spines and spinules. Ventrolateral border of carapace near base of epistome with 3–4 denticles; epistome terminating ventrally in distal spine.

Antennule: peduncular article 1 with ventral spine. Antenna: peduncular articles 1, 3 and 4 with 1, 2 and 3 ventral spines respectively; scale terminating in 2 spinules.

Pereopod 1 subcheliform. Ischium with ventral spine. Merus nearly 3 times as long as broad, bearing dorsal subdistal and 8 large ventral spines. Carpus carrying fine longitudinal groove on upper part of external surface, with ventral subdistal, dorsal subdistal and 2 large mesial distal spines; 7 spines and spinules along or near dorsal margin. Propodus approximately 2.5 times as long as broad, dorsal border bearing 9 spines, mesial surface with 2 longitudinal rows of 5 and 6 spines each with foremost sitting near articulation with dactylus; large slender spine near the middle of ventral margin, smaller spine at its base and another one behind it; fixed finger about one-third as long as dactylus, unarmed. Dactylus with corneous tip, very slight longitudinal dorsal groove on external surface and few small median tubercles mesially.

Pereopod 2: merus with 2 dorsal subdistal spines and 3 spines on proximal third of ventral margin. Carpus bearing 4 spines on dorsal margin and ventral distal spine.

Pereopod 3: merus with dorsal subdistal spine, spinule and 6 spines on ventral margin. Carpus with ventral distal spine. Dactylus carrying few small tubercles dorsally.

Telson slightly shorter than sixth abdominal segment, with very faint inverted U-shaped carina dorsally; posterolateral corners rounded, posterior margin weakly concave medially.

Uropod: exopod rounded, endopod approximately triangular, both little longer than telson; protopod with spinule.

Etymology. The species is named for Gary C. B. Poore who collected the material.

Remarks. The spination of the rostrum, anterolateral border of the carapace and antennal peduncle plus the shape of the telson and uropods place this new species close to *Gebiacantha acanthochela* Sakai, 1967 from Japan. It differs from Sakai's species in:

1, a shorter rostrum with larger infrarostral spines;

2, pereopod 1 more slender and with fewer spines: propodus about 2.5 times as long as broad, armed with 9 dorsal spines and two rows of 5 and 6 mesial spines each (propodus twice as long as broad with 12–13 dorsal spines and three rows of 9–10 mesial spines each in *G. acanthochela*);

3, dactylus of pereopod 1 with an unarmed dorsal margin and a smooth external surface (with 3 proximal tubercles on dorsal margin and a distinct carina on external surface); and

4, propodus of pereopod 2 unarmed dorsally (with a proximal spine).

In the shape and spination of its rostrum and pereopod 1, this new taxon is also similar to *G. arabica* Ngoc-Ho, 1989 from the Gulf of Suez. It differs from the Gulf species in:

1, its larger infrarostral spines;

2, anterolateral border of the carapace armed with 5 spines and spinules (with 2 spinules only in *G. arabica*);

3, antennal articles 1 and 3 bear 1 and 2 spines respectively (0, 1 spine respectively in *G. arabica*); and

4, the different shape of the uropods.

Gebiacantha priochela Sakai

Figures 7, 8

Gebiacantha priochela Sakai, 1989: 100–105, figs 7–9.

Material examined. Western Australia, North-west Shelf (19°48'S, 117°45'E), D. Tranter, 0100 h, 8 Nov 1983,

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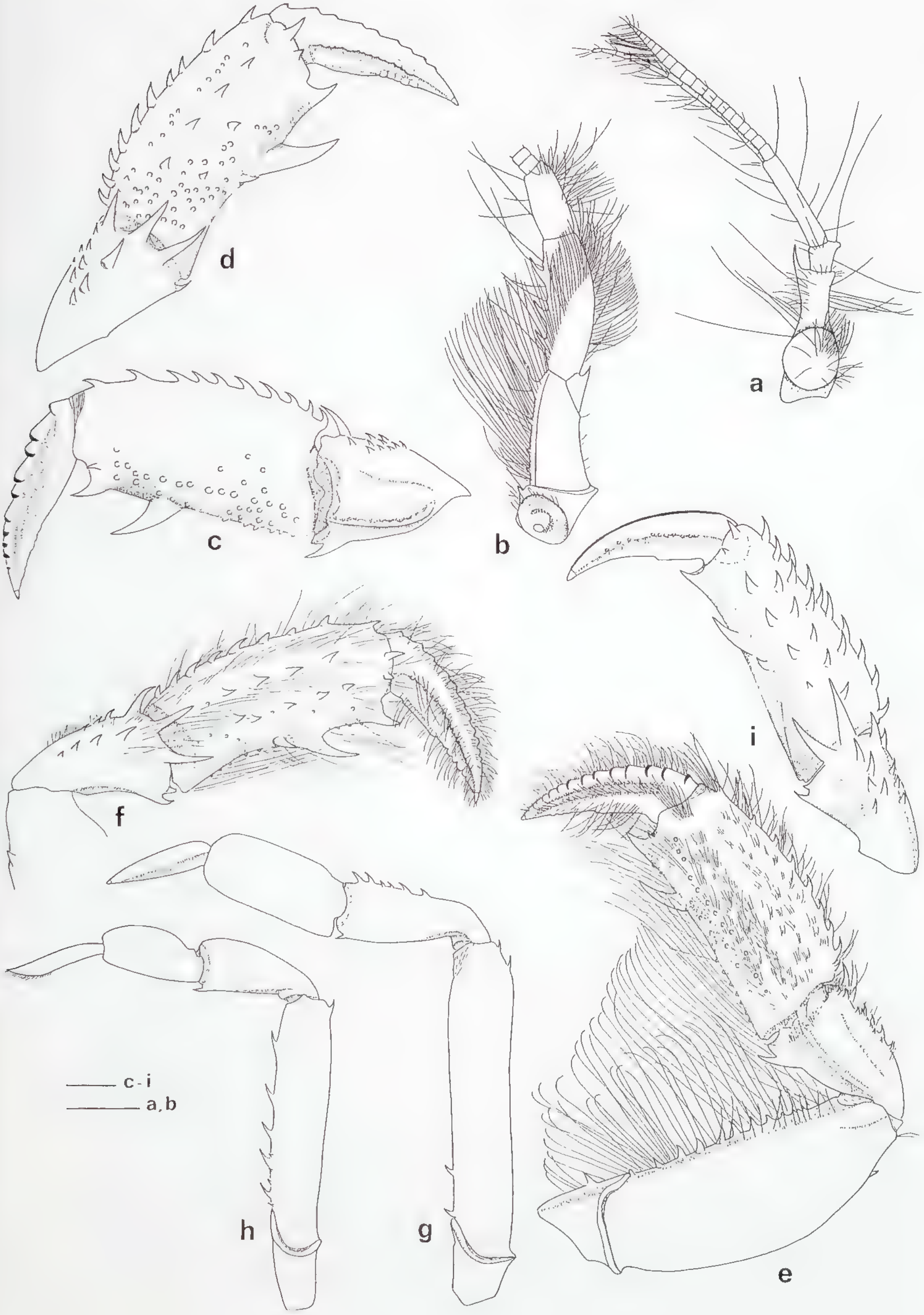
Figure 8. *Gebiacantha priochela* Sakai. Male, tl. 27 mm (MNHN-Th 1252): a, b. Male, tl. 26 mm (MNHN-Th 1252): c, d. Male, tl. 28.5 mm (NMV J17920): e, f. Male, tl. 27 mm (MNHN-Th 1250): g, h. *Gebiacantha plantae* (Sakai). Paratype male, cl. 12 mm (MNHN-Th 569): i.

a, antennule; b, antenna; c and e, distal part of pereopod 1 and whole appendage respectively, external view; d, f and i, distal part of pereopod 1, mesial view; g and h, pereopod 2 and 3.

Scale lines: 1 mm.


d
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surface dip net (water depth 50 m), NMV J22663 (1 male, cl. 10 mm, tl. 28 mm); NMV J22664 (2 males, cl. 10.5 mm, tl. 28 mm and 2 females, cl. 9.5 mm, tl. 26 mm); MNHN-Th 1250 (1 male, cl. 10 mm, tl. 27 mm and 1 female, cl. 9 mm, tl 25 mm); NMV J17913 (10 males, cl. 9.5–10.5 mm, tl. 25.5–28 mm); NMV J17914 (25 females, cl. 6.5–10.5 mm, tl. 20.5–28 mm); MNHN-Th 1251 (6 males, cl. 9.5–10.5 mm, tl. 25.5–28 mm and 8 females, cl. 6.5–10 mm, tl. 20.5–28 mm).

Western Australia. North-west Shelf, between Dampier and Port Hedland (19°56.8'S, 117°53.4'E), CSIRO Division of Fisheries, trawl, 22 Apr 1983 (stn NWA 116), 42 m, NMV J17922 (4 males, cl. 9.5–11 mm, tl. 25.5–28.5 mm).

Queensland, NE of Townsville (19°3'S, 146°52'E), 23 m, muddy sand, dredge, G. C. B. Poore and H. Lew Ton on RV *The Harry Messel*, 24 Nov 1982, NMV J17916 (2 males, cl. 13.5–14.5 mm, tl. 36–38.5 mm). 45 km NE of Townsville, 27 m, A. Birtles and P. Arnold, 10 Apr 1979, NMV J17920 (3 males, cl. 10.5–11.5 mm, tl. 26.5–28.5 mm); MNHN-Th 1252 (2 males, cl. 10–10.5 mm, tl. 26–27 mm and 1 female, cl. 10 mm, tl. 25.5 mm); NMV J22665 (1 female, cl. 9 mm, tl 24 mm and 5 males, cl. 9.5–10.5 mm, tl. 24.5–26 mm); NMV J22666 (1 male, cl. 11.5 mm, tl. 29 mm).

Description. Rostrum rounded anteriorly, about as long as wide at base, projecting far beyond eyes; dorsal surface with very faint median longitudinal groove and 6–7 large spiniform teeth on each lateral margin; ventral surface with 2–3 (rarely 4) slender spines pointing forward. Gastric region bearing small rounded tubercles, 2–5 of them on top of faint median carina on posterior half, others alongside lateral grooves; lateral ridges carrying 7–8 spiniform teeth. Anterolateral border of carapace with 5–7 spines and spinules. Cervical groove deep, with large spine on each side, near intersection with linea thalassinica, latter extending to posterior border of carapace.

Antennule: first peduncular article with large ventral distal spine. Antenna: peduncular article 1, 3 and 4 bearing respectively 1, 2–4 and 3–4 spines, scale terminating in 2 spinules.

Pereopod 1 subcheliform, sexually dimorphic.

Male of 'stout type' (figs 7c, 7d). Ischium with ventral spine. Merus about 2.5 times as long as broad at midlength, dorsal margin with subdistal spine and 3–6 small tubercles in median part; ventral margin bearing 5–7 large spines in proximal two-thirds and 5–7 spinules distally. Carpus with external longitudinal tuberculate crest terminating in pointed tip in lower half and fine longitudinal groove in upper part; 4 large subdistal spines: one ventral, 1 dorsal and 2 mesial; upper mesial spine followed posteriorly by 3–5 smaller ones, and 7–9 spinules externally, near dorsal carpal margin. Propodus approximately twice as long as broad, dorsal margin bearing 9–11 spines and few spinules or tubercles; ventral margin denticulate, with spine near middle and much larger one in front of it; external surface carrying fine longitudinal groove near dorsal margin, proximal rounded tubercles medially, longitudinal row of large tubercles together with smaller ones and spinules in lower part; ventral subdistal spine just above fixed finger; mesial surface bearing numerous small tubercles, some spinuliform, and large spine in middle of distal border, near articulation with dactylus; fixed finger very small, hardly resembling spine. Dactylus about two-thirds length of propodus, with corneous tip; dorsal margin carrying longitudinal row of quadrate plates, larger ones proximally and with corneous anterior edge; weak median smooth longitudinal carena on external surface and longitudinal row of small tubercles mesially; cutting edge dentate on whole extent, bearing, in addition, 7–8 faint, semicircular teeth on distal half of mesial surface.

Males of 'slender type' (figs 8c, 8d, 8e, 8f). Merus without dorsal tubercles. Propodus over twice as long as broad at midlength (figs 8e, 8f) or slightly stouter (figs 8c, 8d) with 9–11 spines on dorsal margin, variable number of tubercles and large spine near middle of ventral margin; external surface with small tubercles in ventral part, many in longitudinal row and distal spinule near base of fixed finger; mesial surface carrying 2 longitudinal rows of spines and variable number of tubercles; 2 distal spines near articulation with dactylus and ventral spine behind large one of ventral border; fixed finger about one-fourth as long as dactylus, cutting edge unarmed. Dactylus as in 'stout type'.

Females (figs 7e, 7f). Pereopod 1 more slender than in males. Ischium with ventral spine. Merus, about 3 times as long as broad, carrying dorsal subdistal spine, 5–6 proximal spines and 6–8 spinules distally on ventral margin. Carpus, as in males, with ventral, dorsal and 2 mesial subdistal spines; upper mesial spine followed posteriorly by 4–5 smaller ones and external to them, 6–9 spines or spinules; smooth longitudinal crest in lower half and fine longitudinal groove in upper half of external surface. Propodus about 2.5 times as long as broad at midlength, with 9–11 spines on dorsal margin; ventral margin with few tubercles proximally and large spine near distal third; external surface unarmed except for small subdistal spine near base of fixed finger; 1–2 longitudinal rows of spines on mesial surface, lower one with 1–3 spines; large subdistal spine near articulation with dactylus and another just behind large ventral spine; fixed

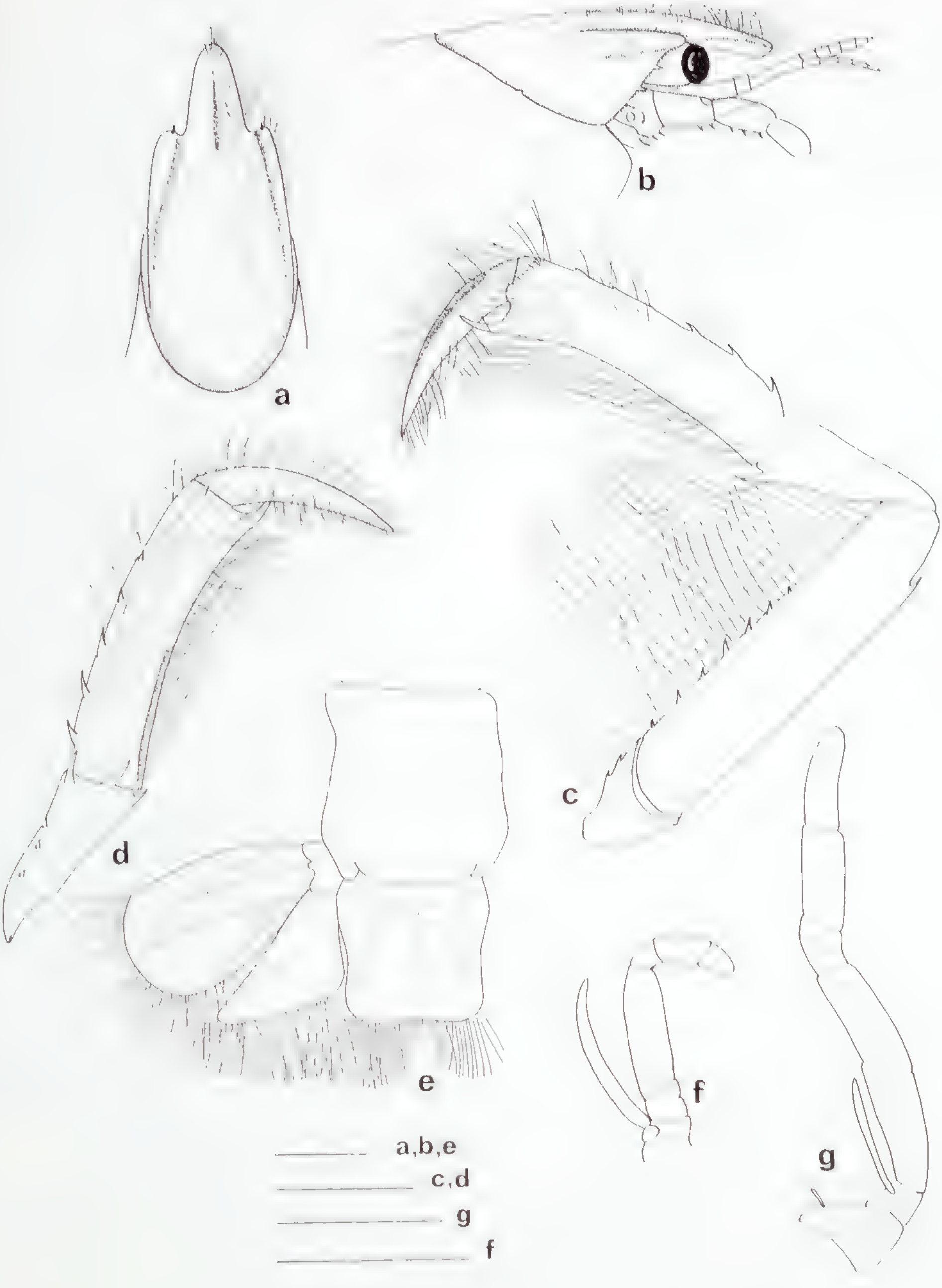

Figure 9. *Upogebia anacanthus* sp. nov. Holotype, male, tl. 7.5 mm (NMV J22668): a–e. Juv., tl. 6 mm (NMV J22670): f, g.
a and b, anterior part of carapace, dorsal and lateral view; c, pereopod 1, external view; d, distal part of pereopod 1, mesial view; e, telson and left uropod; f, maxilliped 2; g: maxilliped 3.
Scale lines: 0.5 mm.

finger longer than in males and about one-third as long as dactylus, cutting edge unarmed. Dactylus with corneous tip and corneous tubercles on dorsal margin; fine tuberculate crest on external surface and few small tubercles on mesial surface, cutting edge smooth.

Pereopod 2: merus bearing 1–2 dorsal subdistal spines and 1–3 spines on proximal half of ventral margin. Carpus with 3–6 dorsal and ventral subdistal spine. Propodus approximately rectangular, dorsal and ventral margins nearly parallel, unarmed. Dactylus with corneous tip.

Pereopod 3: merus with dorsal subdistal spine, 5–8 spines and number of scattered proximal spinules and tubercles on ventral margin. Carpus with ventral distal spine. Dactylus bearing pectiform setae distally on ventral margin.

Telson approximally as long as sixth abdominal segment and slightly broader than long, with faint inverted U-shaped carina; lateral borders convex in proximal third; posterolateral angles rounded, posterior border weakly concave medially.

Uropod: exopod approximately triangular, endopod trapezoidal, protopod with spinule hanging over endopod.

Remarks. This taxon can be placed within the first group of *Gebiacantha* species proposed by Ngoc-Ho (1989). These are species with relatively short uropods whose exopod hardly overeaches the telson and with a nearly straight posterior margin; the posterior border of the telson is weakly concave medially. Within the group, the most closely related to *G. priochela* is *G. plantae* (Sakai, 1982). Furthermore, examination of the paratypes of the latter species revealed a male with pereopod 1 (fig. 8i) resembling in many ways that of a female (see Ngoc-Ho, 1989: fig. 3e). This male of *G. plantae* of the 'slender type' differs from the holotype male (Ngoc-Ho, 1989: figs 3c, 3d), which seems of the 'stout type', in having more spines on the propodal mesial surface and a longer fixed finger.

Both species, *G. priochela* and *G. plantae*, therefore have two types of males. Table 1 shows that although the 'slender' male pereopod 1 is very similar to that of the female in *G. plantae*, it differs by the presence of a dorsal corneous carina on the dactylus, a feature it shares with the male of the 'stout type'.

G. priochela can be distinguished from *G. plantae* in having more spines on the anterolateral border of the carapace and on the third article of the antenna. Furthermore, in males of either the 'stout' or 'slender' type, the dactylus of pereopod 1 allows easy differentiation of the two species; its dorsal border bears quadrate plates with anterior corneous edge in *G. priochela*, a longitudinal corneous carina in *G. plantae*. These probably represent a male stridulating apparatus in both species. Females of the new taxon differ from those of *G. plantae* in having fewer spines on the propodal mesial surface of pereopod 1.

Morphology of the female pereopod 1 is similar in *G. plantae*, *G. priochela* and a few other species of *Gebiacantha* such as *G. talismani*, *G. ceratophora* and *G. reunionensis*. In all, this appendage is slender with the propodus nearly three times as long as broad at midlength, bearing 1–3 rows of spines on the mesial surface. The dactylus is also slender, over half the length of the propodus, often with a tuberculate or dentate dorsal border and with tubercles both externally and mesially. The similarity in the pereopod 1 may be related to ecology but this is unknown.

The existence of two types of males in upogebids has been reported in *Upogebia pugnax* De Man, 1905 (Ngoc-Ho, 1991), *U. edulis* Ngoc-Ho and Chan, 1992. Usually males of both types come from the same locality. Only in *G. priochela* are they imperfectly geographically separated. Most males of the 'stout type' were collected on the North-west Shelf but three were taken in Queensland with males of the 'slender type'. Preserved in 75% alcohol, western specimens have a whitish and firm carapace while it is pink-brown and softer in most eastern ones. This difference in colour and firmness of the carapace may be due to habitat or fixation conditions.

Some specimens of *G. priochela* were collected on the North-west Shelf with a surface dip net at 0100 h where the water was 50m deep. They were probably attracted to the surface by light and the water depth indicates that they are capable of effective swimming.

Upogebia Leach, 1814

Upogebia anacanthus sp. nov.

Figure 9

Material examined. Holotype. Queensland, NE of Townsville (18°43'S, 146°45'E), 34m, muddy sand, dredge, G. C. B. Poore and H. M. Lew Ton on RV *The Harry Messel*, 24 Nov 1982 (stn AIMS 4), NMV J22668 (male juv., cl. 3mm, tl. 7.5mm).

Paratype. Type locality, MNHN-Th 1253 (male juv. cl. 2.5mm, tl. 6mm).

Other material. Pandora Reef (18°49'S, 146°26'E), deep

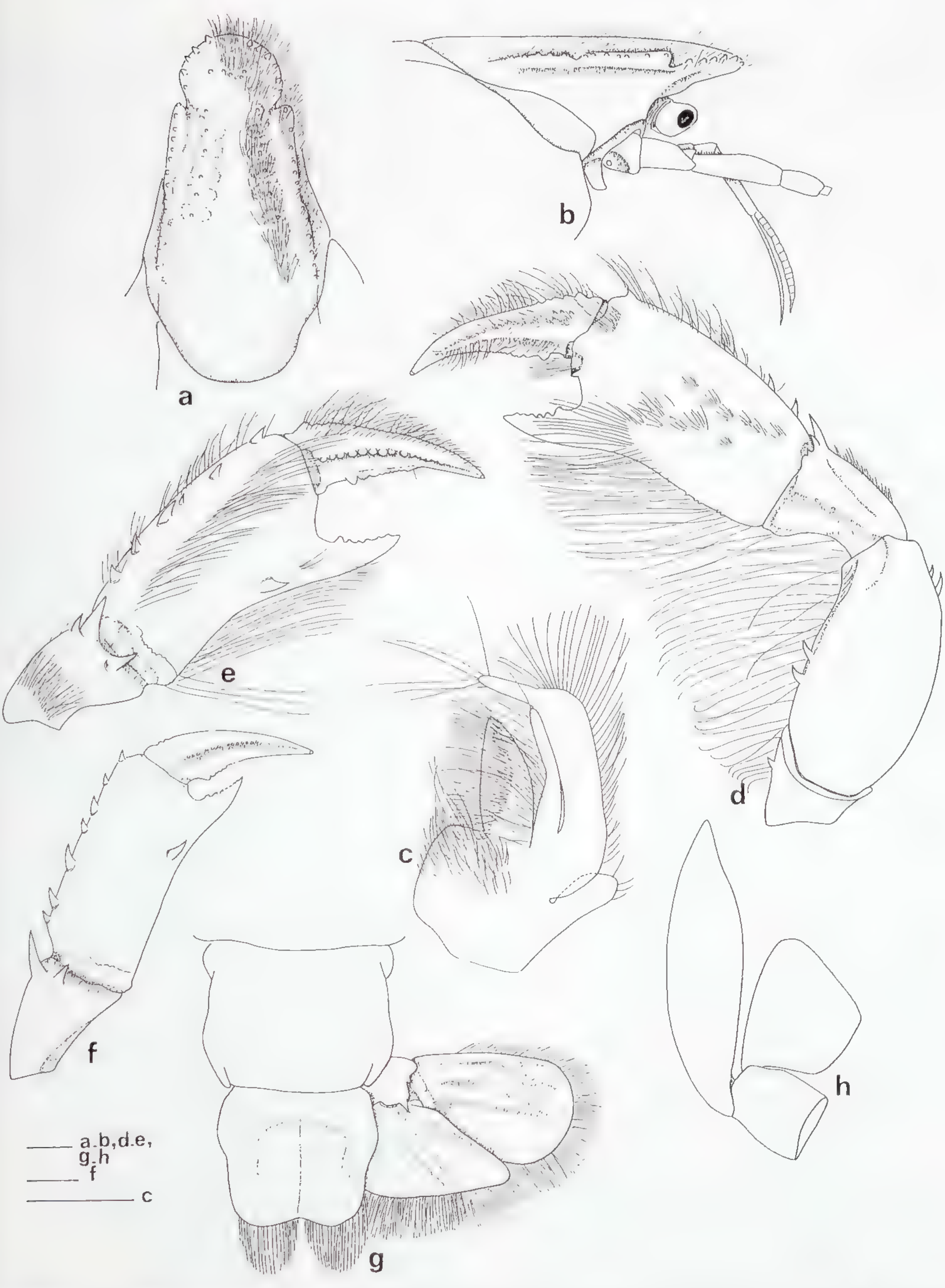

Figure 10. *Upogebia giralia* Poore and Griffin. Male, tl. 31.5 mm: a–e, h. Male, tl. 29.5 mm: g. Female, tl. 31 mm: f (MNHN-Th 1249).

a, b, anterior part of carapace in dorsal and lateral view; c, maxilliped 1; d, pereopod 1, external view; e and f, distal articles of same, mesial view; g, telson and left uropod; h, pleopod 2.

Scale lines: 1 mm.

leeward slope, 12 m, sediment cover, epifauna scarce, M. Riddle, corer, Feb 1986, NMV J22670 (5 juv. without P1, cl. 2–2.5 mm, tl. 5–6 mm); 10 m, transition between coral and sediment, May 1986, NMV J22671 (2 juv. without P1, cl. 2 mm, tl. 5 mm and 6 mm).

Description. Rostrum rounded apically, about 1.5 times as long as broad at base and twice as long as eye-stalk; lateral margins tapering distally, unarmed; fine longitudinal median groove on dorsal surface. Gastric region also unarmed, lateral grooves long and fine, lateral ridges terminating in small distal spinule in holotype, unarmed in paratype. Anterolateral border of carapace with 2 spinules. Cervical groove moderately deep with lateral spinule on each side; linea thalassinica invisible.

Antennule: peduncule unarmed. Antenna: peduncular article 1, 3 and 4 bearing 1–2, 2 and 3 spinules respectively.

Epistome with 2 spinules at apex.

Maxillipeds 1–3 with epipod; exopod of maxillipeds 2 and 3 (figs 9f, 9g), unusual in family, provided only with basal article and without flagellum.

Pereopod 1 subcheliform and slender. Ischium with 2 ventral spinules. Dorsal subdistal and 6–7 ventral spines on merus. Carpus bearing small ventral subdistal, 2 large mesial subdistal spines and 3 spinules along dorsal margin. Propodus more than 4 times as long as broad, mesial surface with 5 spines on dorsal margin, larger ones proximally, and distal spinule near articulation with dactylus; fixed finger about quarter length of dactylus, slender, tip upturned, cutting edge unarmed. Dactylus two-thirds as long as propodus with faint longitudinal dorsal groove on external surface, unarmed.

Pereopod 2: merus with 2 dorsal subdistal and 6 ventral spinules . Carpus bearing dorsal and ventral distal spinule.

Telson approximately square, posterolateral angles rounded and posterior margin nearly straight; very faint inverted U-shaped carina and faint longitudinal median groove on dorsal surface.

Uropod: exopod longer than telson, posterior border rounded, endopod approximately triangular, protopod with rounded tubercle.

Etymology. The species name refers to the absence of teeth or spines from the rostrum.

Remarks. In the shape of its rostrum and pereopod 1, *Upogebia anacanthus* is similar to *U. contigua* Bozic and de Saint Laurent, 1972 from the Gulf of Guinea. It differs from the latter species in having more spines on the anterolateral border of the carapace and on the propodus of pereopod 1. Besides, the exopods of maxillipeds 1 and 3 have no flagellum in *U. anacanthus* and its uropods are hardly longer than the telson whilst they are nearly twice the length of the telson in *U. contigua.*

This new taxon has characteristics bringing it near to *Gebiacantha* Ngoc-Ho. These are the spination of the anterolateral border of carapace and antennal peduncle and also the shape of pereopod 1 and uropods. Nevertheless, *U. anacanthus* has no infrarostral spines and can be differentiated from species of *Gebiacantha* by the absence of a flagellum on maxillipeds 2, 3 and by its quadrate telson with a nearly straight posterior margin.

Upogebia giralia Poore and Griffin

Figure 10

Upogebia giralia Poore and Griffin, 1979: 297, fig. 49.

Material examined. Holotype. Western Australia, Learmonth, mangroves, A. M. Douglas and G. F. Mees, 20 May 1960, WAM 123–75 (male, broken, cl. 14 mm).

Paratype. Same locality, WAM 124–75 (female, cl. 6 mm).

Other material. Queensland. Harmer Creek (11°50'S, 142°57'E), P. Davie and J. Short, 31 Oct 1990, QM W16830 (7 males, cl. 7–10 mm, tl. 18.5–30 mm; 9 females, 2 ovig., 1 without abdomen, cl. 7–10 mm, tl. 20–30 mm); MNHN-Th 1249 (2 males, cl. 10–12 mm, tl. 29.5–31.5 mm; 2 ovig. females, cl. 10–10.5 mm, tl. 30–31 mm).

Northern Territory. Mickitts Creek, near Darwin, in thick mud, P. Davie, 30 Jun 1982, QM W10906 (1 male broken, cl. 7 mm, 1 female broken, cl. 12 mm).

Description. Rostrum broadly rounded anteriorly, slightly longer than broad at base and twice as long as eye stalk, with 5–6 small spiniform teeth on each lateral side; dorsal surface with few tubercles. Gastric region with small tubercles alongside shallow and narrow lateral grooves; fine lateral ridges bearing 13–14 tubercles. Cervical groove deep, linea thalassinica extending to posterior border of carapace. Anterolateral border of carapace unarmed.

Antennule and antenna, peduncle unarmed.

Mandibule without anteromesial tooth.

Maxilliped 1 (fig. 10c) with large epipod.

Maxilliped 3 without epipod.

Paired arthrobranchs of type C, with 2 tubular filaments on each side of rachis on maxilliped 3 to pereopod 4; single pleurobranch on thoracic segment of pereopod 5.

Pereopod 1: Ischium with ventral spine. Merus bearing 1 or (seldom) 2 dorsal subdistal and 2–4

ventral spines. Carpus with fine longitudinal groove on upper part of external surface and 4 subdistal spines: large dorsal, large mesial and 2 smaller external. Propodus nearly twice as long as broad, stouter and more dilated distally in males than in females with few external rounded tubercles on proximal half of ventral border; distal spine, sharp or obtuse, on external surface between base of fixed finger and dactylus; mesial surface with row of 6–7 dorsal spines and large ventral spine behind fixed finger; fixed finger about half length of dactylus, with 4–6 rounded teeth on cutting edge, larger ones proximally. Dactylus approximately two-thirds as long as propodus, with 3–4 dorsal tubercles, few proximal denticles externally and median tuberculate carina on mesial surface; cutting edge dentate in median part.

Pereopod 2 with dorsal subdistal spine on merus.

Pleopods 2–5: exopod slender, lanceolate; endopod approximately quadrate and two-thirds as long as exopod.

Telson about 1.2 times as broad as long, lateral border convex proximally, posterolateral angles rounded, posterior border concave in median part; very faint inverted U-shaped carina and fine median groove on dorsal surface.

Uropod: endopod trapezoidal; exopod longer than telson, posterior border rounded; protopod with spinule hanging over endopod.

Distribution. Northern Australia from north-west Western Australia, Northern Territory to Northern Queensland.

Remarks. Poore and Griffin (1979) compared *Upogebia giralia* with *U. dromana* Poore and Griffin, 1979, also from Australia as both species have obsolete lateral ridges of the carapace. This species was also considered similar to *U. osiridis* Nobili, 1904 from the Red Sea in the shape of its rostrum.

U. giralia is at present the only known Australian species of *Upogebia* provided with a pleurobranch on the eighth thoracic segment (pereopod 5). Besides this characteristic, it has also pleopods (fig. 10h) whose quadrate endopod has never been reported in Australian upogebiids. The usual morphology of the pleopod in the Upogebiidae is depicted in fig. 7g. Another feature worth being pointed out is the presence of asymmetrical pereopods 1 in a male of tl. 28.5 mm. Its right appendage, much smaller than the left, is probably regenerated, and that is very rarely found in the Upogebiidae. It would seem that these burrowing crustaceans can hardly survive, even temporarily, with a single cheliped.

U. giralia belongs to a group of six upogebiid species characterised by the presence of a pleurobranch on the thoracic segment of the fifth pereopod. They are: *U. africana* (Ortmann, 1894), *U. allobranchus* Ngoc-Ho, 1991, *U. capensis* (Krauss, 1843), *U. giralia* Poore and Griffin, 1979, *U. lenzrichtersi* Sakai, 1982, and *U. stellata* (Montagu, 1808). Their other common characters are: two arthrobranchs, each with two filaments on each side of the rachis (type C, see Ngoc-Ho, 1981) on maxilliped 3 to pereopod 4; mandible with a small mesioanterior tooth or unarmed; epipod on maxillipeds 2–3 or 1–2; pereopod 1 subcheliform; telson slightly broader than long, weakly concave medially; endopod of uropod trapezoidal; exopod with more or less rounded posterior border, a little longer than telson, protopod with a spinule.

On the basis of the epipods on maxillipeds, these species can be divided into two groups:

1. Species without or with a minute (and disregarded) epipod on maxilliped 1, with an epipod on maxillipeds 2 and 3. These include: *U. africana, U. allobranchus, U. capensis, U. lenzrichtersi, U. stellata*. They also share the presence of a spine on the anterolateral border of the carapace and the scale of the antenna terminating in a spinule.

2. Species with a large epipodial lobe on maxilliped 1, without epipod on maxilliped 3. *U. giralia* is at present the only known species of this group. It has no spine on the anterolateral border of the carapace and its antennal scale is unarmed apically. This species has also pleopods with an endopod of unusual quadrangular shape.

Sakai (1982: 105) stated *U. giralia* should be placed in the genus *Wolffogebia* Sakai. Study of new materials of *W. phukettensis* and *W. inermis* has discovered supplementary characters of *Wolffogebia*. (Ngoc-Ho, 1994). *U. giralia* shares with these two:

1, absence of a median longitudinal groove on the rostrum;

2, absence of a spine on the anterolateral margin of the carapace together with a subcheliform perepod 1; and

3, a large epipodial lobe on maxilliped 1, maxilliped 3 without epipod.

Differences are:

1, the rostral median carina (very slight in *W. phukettensis*, type species, and in *W. inermis*) is absent in *U. giralia* and replaced by a narrow longitudinal non-setose area;

2, maxillipeds 2 and 3 with an exopod of usual morphology, terminating in a short flagellum (exopod of maxillipeds 2 and 3 without a flagellum in *W. phukettensis* and *W. inermis*);

3, arthrobranch of type C with double series of small filaments on each side of the rachis (of type A with a single series of large lamellae on each side of the rachis); and

4, pleurobranch on thoracic segment of pereopod 5 (pleurobranch absent).

Differences in maxillipeds 2 and 3 morphology, in the structure of the arthrobranchs and especially in the posession of an extra pleurobranch on pereopod 5 are considered of great evolutionary importance and separate *U. giralia* from other species of *Wolffogebia*. *U. giralia* is more likely to take its place within the small group of six *Upogebia* species mentioned above. Nevertheless, absence of median rostral groove and the unusually coupled characters, subcheliform pereopod 1 and anterolateral border of carapace unarmed, suggest similarity of *U. giralia* and others of the group to *Wolffogebia*.

Upogebia tractabilis (Hale)

Figure 11

Upogebia (*Calliadne*) *tractabilis* Hale, 1941: 276–277, fig. 11. — Poore and Griffin, 1979: 307–309, fig. 55.

Upogebia (*Upogebia*) *tractabilis*. — Sakai, 1982: 16–17, figs 1e, 2c–e.

Upogebia tractabilis. — Sakai, 1993: 91.

Material examined. Holotype. South Australia, St Vincent Gulf, SAMA C888 (ovig. female, cl. 7 mm, tl. 21 mm much damaged, broken into two pieces).

Other material. Same locality, SAMA C4103 (14 males, cl. 2.5–5.5 mm, tl. 7–14.5 mm, 20 females, 11 ovig., cl. 4–6 mm, tl. 9.5–17.5 mm); MNHN-Th 1266 (1 male, cl. 4.5 mm, tl. 13 mm, 2 ovig. females, cl. 5 mm and 5.5 mm, tl. 15 mm and 16 mm).

Queensland. South side of Seaforth I. (20°28'S, 149°02'E), subtidal in staghorn coral, P. Davie and J. Short, 24 Mar 1987, QM W14407 (1 female juv., cl. 3 mm, tl. 8.5 mm).

Description. Rostrum triangular, short, about half as long as broad at base and hardly reaching extremity of eye, with median groove and 4–5 spinules on each lateral border. Gastric region bearing small rounded tubercles with most alongside shallow lateral grooves; lateral ridges each with distal spinule and 7–12 spiniform tubercles. Anterolateral border of carapace unarmed. Cervical groove moderately deep and linea thalassinica invisible posterior to it.

Maxilliped 1 (fig. 11e) with exopod flattened distally bearing setae of 2 lengths, the longer on external border; epipod absent.

Maxilliped 2 (fig. 11f) with minute epipod standing upright on coxa bearing 1 or 2 setae.

Maxilliped 3 without epipod.

Pereopod 1 cheliform. Ischium with 0–1 ventral spine; 4–8 ventral spines and spinules on merus. Carpus with ventral spine and dorsal subdistal spinule on mesial surface. Propodus, about twice as long as broad, often with small subdistal spinule on upper border; fixed finger slender, unarmed. Dactylus, about half length of propodus, with incurved tip and 4–6 denticles in median part of cutting edge.

Telson longer than sixth abdominal segment and approximately as long as broad; posterior border rounded in juvenile specimen from Queensland (fig. 11c), slightly convex in others, faint inverted U-shaped carina dorsally.

Uropod: endopod shorter than telson, posterior margin nearly straight; exopod slightly longer than telson, with proximal spinule, posterior margin rounded; protopod also with spinule.

Distribution. Australia (St Vincent Gulf and Queensland).

Remarks. The holotype of *U. tractabilis* was examined with material captured at the same time by Hale, and a few figures are (figs 11d, 11e, 11f) added to those given in the original description (Hale, 1941: fig. 11). There is a mistake in the lettering of Hale's fig. 11c and 11d which should be inverted. Fig. 11c actually represents 'the inner view of the left chela' on which the mesiodistal spine of the carpus is visible. The outer view of the same cheliped is here depicted in fig. 11d.

Hale reported the presence of a subdistal spine on the upper border of the cheliped propodus which can be seen in the holotype (with some difficulty on the left which is slightly damaged at that level) and is often present in the other material captured at the same locality (SAMA C 4103).

The Queensland specimen studied agrees with the holotype and Hale's other material in spite of the rounded posterior border of the telson which is probably due to its young age. It especially agrees in the uncommon morphology of maxilliped 1 whose exopod is slightly flattened distally with setae of two lengths and maxilliped 2 whose epipod is small and not folded laterally as compared with what is usually reported in the family, e.g. in *U. laemanu* (fig. 12d).

Another species with similar maxillipeds 1 and 2 (epipod on maxilliped 2 is here slightly larger) and coming from a nearby area is the New Caledonian *U. stenorhynchus* Ngoc-Ho (1991:

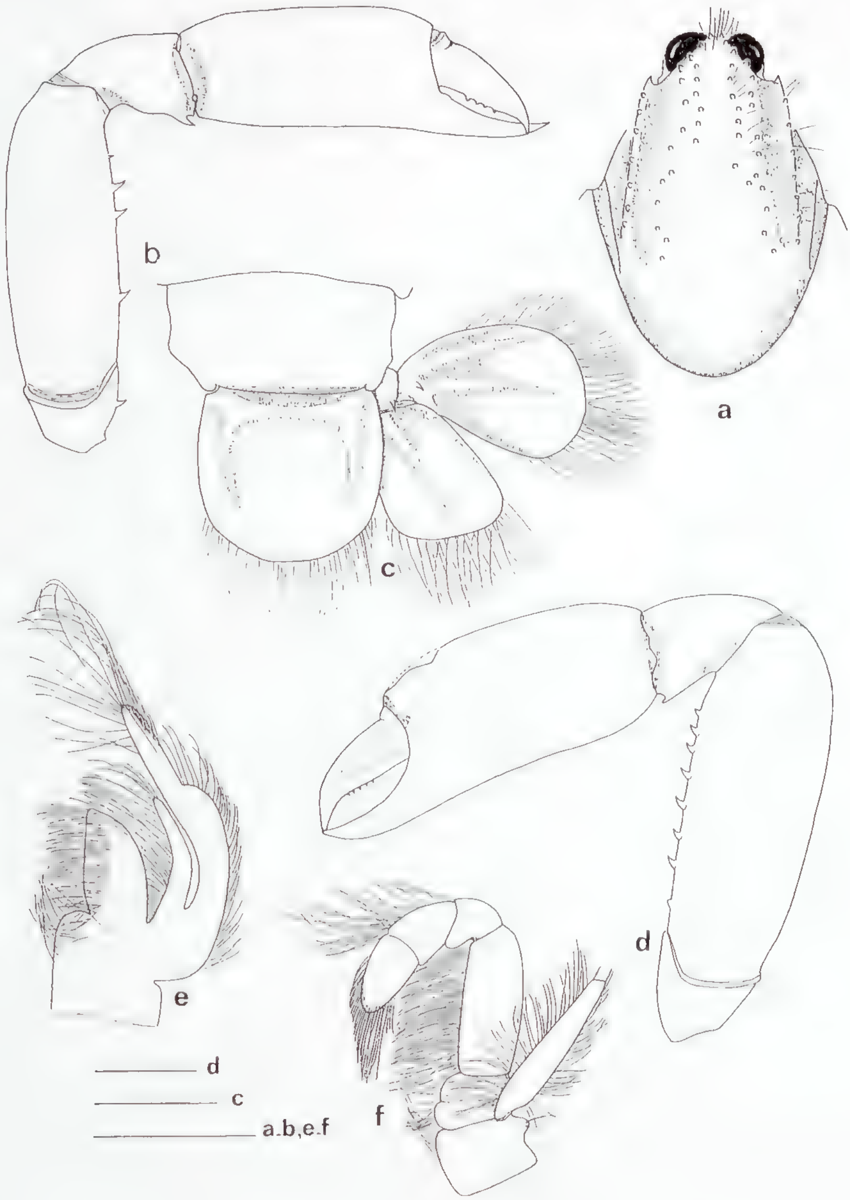

Figure 11. *Upogebia tractabilis* Hale. Female juv., tl. 8.5 mm (QM W14407): a–c. Holotype, ovig. female (SAMA C888): d. Ovig. female, tl. 15 mm (MNHN-Th 1266): e, f.

a, anterior part of carapace, dorsal view; b and d, pereopod 1, external view; c, telson and right uropod; e and f, maxilliped 1 and 2 respectively.

Scale lines: 1 mm.

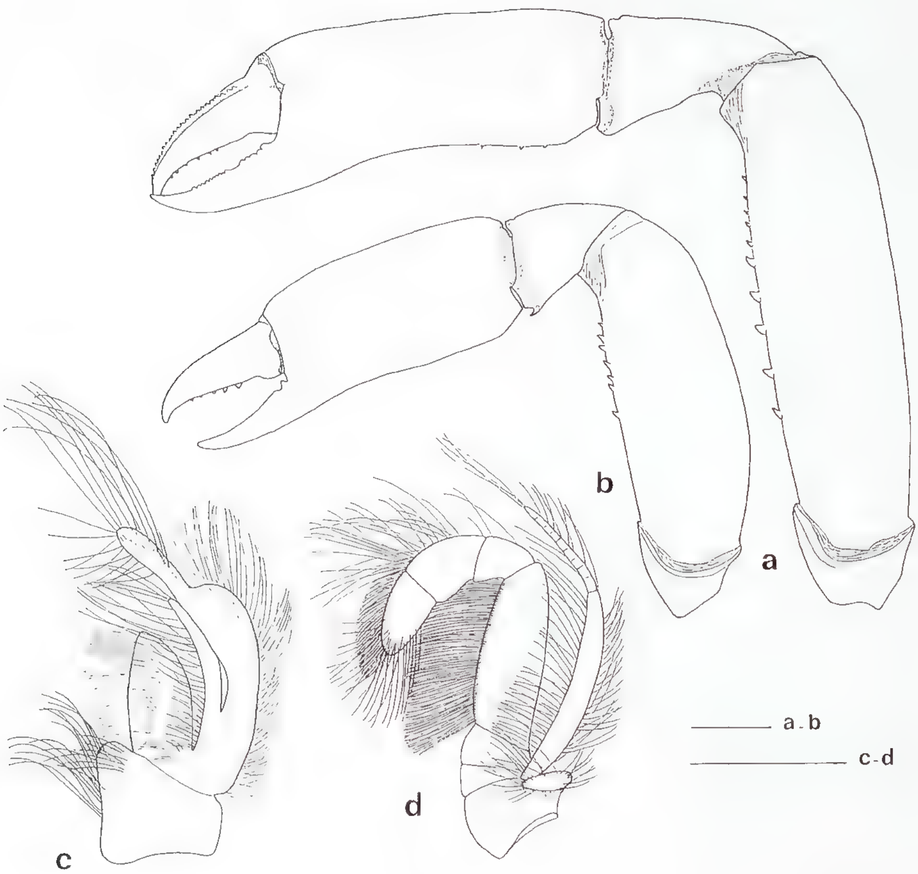

Figure 12. *Upogebia balmaorum* Ngoc-Ho. Paratype, ovig. female, tl. 32.5 mm (MNHN-Th 1064): a, pereopod 1, external view.

Upogebia laemanu Ngoc-Ho. Paratype, ovig. female, tl. 24.5 mm (MNHN-Th 906): b, pereopod 1, external view; c and d, maxilliped 1 and 2 respectively.

Scale lines: 1 mm.

307, fig. 11). It is simlar to *U. tractabilis* in all cephalic appendages, the three maxillipeds and uropods. They differ in:

1, rostrum longer and narrower in *U. stenorhynchus*;

2, different spinulation of male pereopod 1: lower border of merus with spinules or granules in *U. stenorhynchus* (with spines in *U. tractabilis*); propodus with ventral tubercles (smooth); fixed finger with 6–7 teeth on proximal half (unarmed); dactylus with a proximal dorsal tooth, another proximal tooth on cutting edge, mesial surface with a median row of rounded tubercles (smooth upper border, 2–4 teeth in median part of cutting edge, mesial surface unarmed); and

3, telson with rounded posterior border (with nearly straight posterior border in adults).

Sakai (1993) synonymised *U. balmaorum* Ngoc-Ho, 1990 and *U. laemanu* Ngoc-Ho, 1990 from the Seychelles with *U. tractabilis*. These three are apparently closely related but comparison of the type material of *U. tractabilis* with those of the two Seychelles' species confirms their distinctiveness. Table I in Ngoc-Ho (1990) gave the main differentiating characters between the three; the following can be added.

Fig. 11d and Figs 12a, 12b represent pereopods 1 of the holotype of *U. tractabilis* (tl. 21 mm) and paratypes of *U. balmaorum* (tl. 32.5 mm), *U. laemanu* (tl. 24.5 mm), all ovigerous females. They show that pereopod 1 of *U. balmaorum* is much more slender, has numerous ventral meral spines, an unarmed carpus and distinctive spinulation on its dactylus and fixed finger. More similarity can be found between pereopods 1 of the two other species, but *U. tractabilis* can be differentiated from *U. laemanu* and *U. balmaorum* on the maxilliped 2 as shown below.

All three possess a maxilliped 1 (fig. 11e, 12c) without epipod and an unusual exopod slightly enlarged distally and bearing setae of two lengths. Maxilliped 2 in both *U. balmaorum* and *U. laemanu* (fig. 12d) has the ordinary morphology of most upogebiid species, especially the relatively large epipod folded laterally and provided with numerous setae. In contrast, maxilliped 2 in *U. tractabilis* (fig. 11f) has a shape so far reported in very few species, that is, its minute unfolded epipod bears almost no setae.

As stated previously (Ngoc-Ho, 1989), variation in upogebiid mouth appendages or branchial structure is probably of evolutionary significance and can be of taxonomic value. The difference in the maxilliped 2 morphology, i.e., the quasi-absence of an epipod on maxilliped 2 of the Australian species, is likely to show that *U. tractabilis* on the one hand and *U. balmaorum* and *U. laemanu* on the other are in different phylogenetic groups. Is is therefore concluded that *U. tractabilis, U. laemanu* and *U. bakmaorum* are distinct species.

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A PHYLOGENY OF THE FAMILIES OF THALASSINIDEA (CRUSTACEA: DECAPODA) WITH KEYS TO FAMILIES AND GENERA

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Abstract

Poore, G.C.B., 1994. A phylogeny of the families of Thalassinidea (Crustacea: Decapoda) with keys to families and genera. *Memoirs of the Museum of Victoria* 54: 79–120.

The confused taxonomy of the Thalassinidea (73 genera recognised here) is briefly reviewed. States of 93 characters are discussed with reference to five outgroup genera of reptant decapods. The linea thalassinica is concluded to be homologous with the linea anomurica of Anomura. Its loss in Axioidea is thought secondarily derived. Burrowing behaviour in callianassoids is coincident with loss of the interaction between the posterior margin of the carapace and anterolateral lobes on abdominal somite 1, and with loss of abdominal pleura. Characters from gills, mouthparts and pereopods are discussed. Pereopodal spiniform setae are a unifying feature of some axioids. Auxiliary surfaces on the margins of pleopods of *Callianidea* and *Michelea* are not homologous. Setal-rows, once thought to unite several genera into the Callianideidae are shown to be more widespread and this family, as previously conceived, to be polyphyletic.

A computer-aided phylogenetic analysis of the families, represented by 22 genera, has confirmed the monophyly of the infraorder, based largely on the unique possession of a setose lower margin to pereopod 2. The Thalassinidea are divided into three superfamilies: Thalassinoidea and Callianassoidea, more closely related to each other than to Axioidea. The Thalassinoidea contains a single family and single genus, *Thalassina*. Callianassoidea are divided into six families: Laomediidae, Upogebiidae, Callianideidae, Thomassiniidae, Ctenochelidae (paraphyletic), and Callianassidae. Axioidea contain four families: Calocarididae, Axiidae, Strahlaxiidae fam. nov. and Micheleidae.

The new classification differs from that of Borradaile (1903) only in the inclusion of many more taxa. The affinities between families suggested by Gurney (1938), de Saint Laurent (1973), Kensley and Heard (1991) and Sakai (1992a) are not supported.

Diagnoses and keys are presented for the families and all the currently accepted genera, largely based on review of the literature and reference to museum collections.

Contents

Introduction

The decapod infraorder Thalassinidea is a group of families of reptant or "tailed decapods which recall the hermit-crabs in some respects and the lobsters and crawfishes in others" (Borradaile, 1903). A satisfactory diagnosis of the group has never been given in spite of the attention of numerous workers. While preparing a contribution describing several new thalassinidean taxa it became clear that the Thalassinidea had never been unambiguously defined and the relationships between all the families had not been thoroughly investigated.

Several families have been assigned to the Thalassinidea but the number, and the genera contained therein, are somewhat contentious. Seventy-three genera are recognised here but the number of available names is larger. Three families, each well defined but themselves not apparently closely related, are:

Thalassinidae Dana, 1852 with two to four very similar species in one genus (fig. 1a; Poore and Griffin, 1979; Dworschak, 1992; Sakai, 1992a).

Laomediidae Borradaile, 1903 with 15 species in five diverse genera (fig. 1b; Kensley and Heard, 1990); and

Upogebiidae Borradaile, 1903 with over 100 species world-wide in seven quite similar genera (fig. 1c; Sakai, 1982; Ngoc-Ho, 1989; Williams and Ngoc-Ho, 1990; Sakai, 1993);

The monophyly of each of these three families is not disputed and each can be defined by numerous autapomorphies.

The remaining genera have been assigned to at least two and as many as 14 family-level taxa and their classification has been more unstable.

The largest of these families are Axiidae Huxley, 1879 (fig. 3a) and Callianassidae Dana, 1852 (fig. 2c). Both have from time to time included some forms which could not be clearly assigned. One genus, *Calocaris* Bell, 1853, was moved to its own family, Calocarididae Ortmann, 1891, but for most of this century has been treated as a member of the Axiidae. Ortmann's taxonomic judgement was supported by Kensley (1989) but was not followed by Sakai and de Saint Laurent (1989). Kensley (1989) included in the Calocarididae four genera previously included in the Axiidae. Sakai and de Saint Laurent (1989) separated *Coralaxius* Kensley and Gore, 1981 into a new subfamily, Coralaxiinae.

The Callianassidae and the smaller Callianideidae Kossmann, 1880 were first redefined in a modern context by de Saint Laurent (1973) who erected a new subfamily of the former, Thomassiniinae. This work was extended by Manning and Felder (1991, 1992), Manning (1992) and Rodrigues and Manning (1992) who erected four further callianassid subfamilies and several new genera. Manning and Felder (1991) implicitly raised Thomassininae to family rank. They added a new family Ctenochelidae (with three subfamilies) for four atypical genera.

Seven callianideid- and thomassiniid-like genera were grouped into the Callianideidae by Kensley and Heard (1991). Sakai (1992a) added another genus (here treated as a junior synonym of *Callianidea*) and divided the family into four subfamilies. Another is added in this work. Numerous new species are being described in work in progress. The genera of interest are: *Callianidea* Milne Edwards, 1837 (fig. 2a), *Crosniera* Kensley and Heard, 1991, *Marcusiaxius* Rodrigues and Carvalho, 1972 (fig. 3c), *Meticonaxius* De Man, 1905, *Michelea* Kensley and Heard, 1991 (fig. 3b), *Mictaxius* Kensley and Heard, 1991, *Tethisea* gen. nov. and *Thomassinia* de Saint Laurent, 1979a (fig. 2b).

The Thalassinidea have also included from time to time the genera *Enoplometopus* Milne Edwards, 1862 and *Hoplometopus* Holthuis, 1983 in the Axiidae (Balss, 1957; Holthuis, 1983) but these are now removed to their own family and superfamily (de Saint Laurent, 1988).

The definition of the Thalassinidea and the relationships between families, subfamilies and

genera are now uncertain. There are competing definitions of Callianideidae, Thomassiniidae and their subfamilies. Examination of species of Axiidae, Calocarididae, Ctenochelidae and Callianassidae revealed that some of the characters used to define the callianideid and thomassiniid groups are more widespread than hitherto appreciated and that neither the schemes of Kensley and Heard (1991) nor of Sakai (1992a) seem to reflect the phylogeny of the infraorder.

It is the objective of this paper to attempt to define the Thalassinidea and to present a new hypothesis explaining family relationships. The work does not resolve generic definitions or relationships in the Axiidae and Calocarididae [dealt with by Sakai and de Saint Laurent (1989), Kensley (1989, work in progress)], and Callianassidae and Ctenochelidae [dealt with by Manning and Felder (1991, 1992), Manning (1992) and Rodrigues and Manning (1992)] although many taxa in these families have been examined in the course of this study. This need arose from the realisation that these families are not as homogeneous as current usage suggests.

A new classification and diagnoses of the superfamilies and families reflecting these relationships are offered. Keys, based mostly on recently published literature, to the superfamilies, families and genera of Thalassinidea in current use are presented.

Methods

Material for this study comes largely from the Muséum National d'Histoire Naturelle, Paris, and from the Museum of Victoria, Melbourne and checked for general consistency by reviewing the literature. Specimens of the rarest species will be listed in a paper nearing completion.

Hennigian phylogenetic (cladistic) methods were used to generate cladograms as hypotheses of the relationships of thalassinidean families. For families of undisputed monophyly, single genera were chosen for inclusion (Thalassinidae, Laomediidae and Upogebiidae). For others where subfamily relationships are unclear (Callianassidae, Axiidae, Ctenochelidae), or whose generic composition is controversial (Callianideidae, Thomassiniidae, Micheleidae), several or all genera were included in the analysis.

Outgroups were chosen from the reptant Decapoda in order to assess general evolutionary trends. These trends are assumed but are unlikely to be controversial. I contend that the primitive thalassinidean had the general habitus shown by the modern axiids, upogebiids, laomediids or thalassinids rather than by callianassids. In the axiids, for example, the cephalothorax is compact, little shorter than the abdomen, solid, with a prominent rostrum from which originate dorsolateral carinae running on to the carapace. The abdomen is firmly attached to the cephalothorax, has well developed pleura on all somites, and is strongly reflexed. In addition, the second abdominal pleuron overlaps the first anteriorly and the two abdominal somites articulate by means of a lateral condyle (cf. Burkenroad, 1981: 259–260). The pleopods 2–5 are similar and sexually unspecialised, and the pereopods 2–4 are typically cylindrical and linear rather than flattened for digging in soft sediments.

As far as is known axiids live in short burrows in hard or soft sediment, in crevices between rocks, or in cavities in sponges or corals. Kensley and Simmons (1988) described the straight 150-mm-long burrows of their new species *Axiorygma nethertoni*. Pemberton et al. (1976) reported that *Axius serratus* builds burrows up to 3 metres deep. *Calocaris macandrae* (Calocarididae) has also been reported to construct burrows (Atkinson and Taylor, 1988). In general they do not build complex lined burrows in muddy or sandy sediments as is the case for some callianassids (de Vaugelas and de Saint Laurent, 1984; Suchanek et al., 1986), a form of behaviour which is correlated with a more elongate body form, specialised fossorial pereopods, and considerable flexibility between the cephalothorax and first abdominal somites.

Discussion on character transformations is based on the assumption that the compact habitus is primitive and the elongate tube-dwelling habitus is derived. Many of the character transformations used in constructing the phylogeny reflect this assumed change in biology. Loss of rostrum and absence of armature on the carapace, abdomen and limbs seem correlated with a burrowing way of life. No assumption is made on the monophyly of the elongate forms.

The program, HENNIG86, was used to establish generic relationships and in order to derive a practical classification which as closely as possible reflected these relationships. Its results were confirmed with the program PAUP version 2.4 which was used to generate a list of apomorphies for each clade in the chosen tree.

The following sections describe the outgroups, taxa chosen and character transformations, before discussing the results and classification.

Outgroups

The living glypheid, *Neoglyphea inopinata*, described in detail by Forest and de Saint Laurent (1981, 1989) was selected as an outgroup and, because it scored zero (was plesiomorphic) for all characters except one, it became the effective 'ancestor' against which the trees were rooted. The genus *Enoplometopus* Milne Edwards (sometimes considered an axiid) to represent the superfamily Enoplometopoidea de Saint Laurent, 1988 and the nephropid, *Nephropsis stewarti* Wood-Mason, were also included. The Anomura were represented by a species of *Munida* (Galatheidae) and of *Dardanus* (Diogenidae).

Taxa chosen

Twenty-two genera representing at least 12 families or subfamilies were included in the phylogenetic analysis. The species from which data were gathered are listed in parentheses.

Three genera represent monophyletic families which, except for the Laomediidae, are relatively homogeneous: *Upogebia* Leach [*U. darwinii* (Miers) but see also Williams, 1986; Ngoc-Ho, 1989; Le Loeuff and Intès, 1974]; *Laomedia* De Haan [*L. healyi* Yaldwyn and Wear but see also Kensley and Heard, 1990]; and *Thalassina* Latreille [*T. squamifera* De Man].

The remaining families are much more diverse in form and with a complex nomenclature. Genera were selected to cover all nominate families and subfamilies.

The Axiidae (including Coralaxiinae) and Calocarididae include at least 30 genera (Sakai and de Saint Laurent, 1989; Kensley, 1989; Sakai, 1992b) but the monophyly of the two families is still questionable. Six very different genera were chosen: *Axiopsis* Borradaile [*A. serratifrons* Milne Edwards]; *Axius* Leach [*A. stirhynchus* Leach]; *Calocaris* Bell [*C. macandreae* Bell]; *Coralaxius* Kensley and Gore [*C. abelei* Kensley and Gore]; *Spongiaxius* Sakai and de Saint Laurent [an undescribed New Caledonian species]; *Strahlaxius* Sakai and de Saint Laurent [*S. plectrorhynchus* (Strahl)]. Because so few genera were selected from this group, the generic relationships of the family (or families) suggested by the analysis are only a weak hypothesis.

All genera of the Callianideidae in the sense of Kensley and Heard (1991) and Sakai (1992a) were included: *Callianidea* [*C. typa* Milne Edwards and *C. laevicauda* Gill]; *Thomassinia* [*T. gebioides* de Saint Laurent and *T.* sp. nov.]; *Crosniera* Kensley and Heard [*C. minuta* (Rathbun) and *C.* sp. nov.]; *Mictaxius* [*M.* sp. nov.]; *Marcusiaxius* [*M. lemoscastroi* Rodrigues and de Carvalho]; *Meticonaxius* [*M. monodon* De Man]; *Michelea* [*M. leura* (Poore and Griffin)]; *Tethisea* gen. nov. [*T. indica* sp. nov.]. Information for all genera was supplemented by other species examined for another work in preparation.

Four genera were selected from the Ctenochelidae as defined by Manning and Felder, 1991: *Anacalliax* de Saint Laurent [*Anacalliax agassizi* (Biffar)]; *Ctenocheles* Kishinouye [*C. collini* Ward]; *Gourretia* de Saint Laurent [an undescribed species]; *Paracalliax* de Saint Laurent [*P. bollorei* de Saint Laurent].

The Callianassidae were represented by *Trypaea* Dana [*Trypaea australiensis* Dana]. Detailed anatomical descriptions of several callianassid genera can be found in de Saint Laurent and Le Loeuff (1979) and Manning and Felder (1991). In fact, the characters scored were largely consistent throughout most callianassid genera, such as *Callianassa* Leach, *Callichirus* Stimpson and *Glypturus* Stimpson, as revealed by a review of extensive collections in the Museum of Victoria and the Muséum National d'Histoire Naturelle. It was not an objective to investigate the relationships of the genera of this large family, only to determine its affiliation to the other thalassinideans.

Character discussion

Ninety-three characters were used in the analysis and are discussed in turn. All are potential synapomorphic characters (i.e. none is apomorphic for a single genus). Their states are given in Table 1 and the data matrix in Table 2. Generic autapomorphies are not included in these tables.

Carapace, linea thalassinica and rostrum. The linea thalassinica (figs 1a–c, 2b, 2c) is said to characterise the Thalassinidea and much has been made of it in the classification of the families. The acquisition of a well-developed linea thalassinica which supposedly allows the lateral carapace to hinge for ventilation and cleaning of the gills would be of value to an animal in a burrow. Borradaile (1903) used the absence of a linea thalassinica to separate the Axiidae (also burrowers) from the other three families he recognised. However, the homology of the linea thalassinica with the linea anomurica in Anomura has never been convincingly demonstrated. I believe that the linea thalassinica is homologous

throughout the thalassinidean genera in which it occurs and is homologous with the linea anomurica.

Four reference points on the anterior margin of the carapace (e.g. fig. 4m) serve to establish this homology: (1) median rostrum; (2) ocular lobe or spine (lateral to the eyestalk); (3) branchiostegal sclerite (a thickened more or less triangular marginal part of the branchial area attached to the epistome anteriorly, defined by weakly calcified grooves dorsally and ventrally, and to which a transverse muscle attaches posterior to the mouthparts); and (4) anterior branchiostegal lobe (a free lobe of the carapace enclosing the mouthparts anterolaterally). The linea anomurica and linea thalassinica start anteriorly as a line of weak calcification defining the dorsal margin of the branchiostegal sclerite. The cervical groove runs obliquely and converges with it.

The linea thalassinica runs the complete length of the carapace in Thalassinidae (fig. 1a), Laomediidae (fig. 1b), most Callianassidae (fig. 2c) and Ctenochelidae as does the linea anomurica in Galatheidae. In upogebiids the anterolateral margin of the cephalothorax is oblique, the branchiostegal sclerite is some distance posterior to the ocular spine, and the thoracic sternites very short (fig. 1c). As a consequence the linea thalassinica is depressed anterior to the point where the cervical groove meets it. The branchiostegal sclerite is more rounded anteriorly than in the Callianassidae but its relationship to the anterior branchial lobe is the same as in other families. An oblique branchiostegal ridge crosses and strengthens the branchiostegal sclerite and often appears as an extension of the cervical groove. The pattern in upogebiids varies between species and is complicated by failure of the linea to always reach the posterior margin of the carapace. An oblique ridge posteriorly on the branchial flap is variously developed in some species and may appear with an associated groove in place of the posterior section of the linea thalassinica. However, whatever the modification of the linea in more evolved upogebiids, there seems little doubt to me that the upogebiid pattern is primitively much the same as in other thalassinideans.

In Axiidae (figs 3a, 4a), Calocarididae and Micheleidae (figs 3b, c) the front of the carapace is simpler. The rostrum, weak ocular lobe and anterior branchiostegal lobe are clear but a defined branchiostegal sclerite is wanting. A very weak lobe near the base of antenna 2 may indicate its anterodorsal corner in some genera. The linea thalassinica is never visible.

Callianidea (fig. 2a) appears very similar to Axiidae but in one of the species (the most primitive on other counts — pleopodal lamellae, male pleopods), *C. laevicauda*, a short linea thalassinica is present and this is how the genus is scored.

In Thomassiniidae there is a linea thalassinica starting between the rostrum and a dorsolateral lobe next to the eyestalk (figs 4i, j). If this is a homologue of the linea thalassinica the lobe must be interpreted as the remnant of the branchiostegal sclerite and the ocular lobe must be absent. An alternative explanation is that the dorsolateral lobe is homologous to the ocular lobe usually found at that site, the true linea is lost, and the longitudinal groove is a new structure. The first explanation seems the simpler and is preferred.

Characters 1 and 2 in Table 1 describe the grooves on the carapace.

An armed rostrum is a usual feature of reptant decapods and its presence is assumed plesiomorphic. The thalassinidean rostrum is never strongly laterally compressed as in many carideans but is always dorsoventrally flattened or reduced. The most primitive condition is seen in axiids (figs 4a–e) and is similar to that in *Neoglyphea* in the possession of lateral carinae and a median carina which does not reach the anterior apex. Within the Thalassinidea the rostrum takes various forms many of which are probably independently derived from the primitive condition. In several genera, notably in the Callianassidae but also elsewhere, it is very reduced, triangular and shorter than the eyestalks (figs 4l, m; character 3); in others there is secondarily a spike-like rostrum (fig. 4i: character 4) and in many genera loss of armature (character 5).

Upogebia and *Thalassina* share a trilobed 'rostrum' of which the most lateral carinae are possibly derived from a ridge running back from the ocular spine. The origin of this cannot be seen in other reptants but the homologies of the structures involved are suggested by the possession of sublateral carinae meeting at the apex of the true rostrum and medial to the most lateral (ocular) ridges (figs 4o–q; character 6). The sides of the rostrum generally continue back on to the carapace as lateral carinae usually fringed by setae. Loss of the carinae in several genera is considered apomorphic (figs 4i–l; character 7). The median rostral carina seen in *Neoglyphea* is frequently lost (character 8).

In the Ctenochelidae the dorsal organ (see

Martin and Laverack, 1992, for a review of the structure and physiological functions of this sense organ) is raised on a cardiac prominence (Manning and Felder, 1991) (character 9).

Carapace-abdomen articulation. Life in long burrows demands a more elongate and flexible habitus than in a typical shrimp. This is best seen in the degree of articulation between the cephalothorax and abdominal somite 1. In the shrimp-like forms a pair of prominent anterolateral lobes on abdominal somite 1 ride on a thickened posterior margin of the cephalothorax and maintain the relative positions of the carapace and pleon. All reptants, such as *Neoglyphea inopinata*, all nephropids and astacideans, possess these anterolateral lobes in one form or another so they are undoubted plesiomorphies within Reptantia. These last named groups possess a posterior carapace margin which is regularly convex mid-dorsally and differs from that in many thalassinideans. In some thalassinidean families the posterior margin is similar and tripartite: on each side of the median convexity is a strong posterolateral lobe whose margin is strengthened by a smooth ridge on which the anterolateral lobes of abdominal somite 1 ride (figs 7a–d). Chace and Kensley (1992) discussed a similar arrangement in the alpheid shrimps and defined a 'cardiac notch' in this family. The pattern in the Thalassinidea is not thought homologous. The medial portion may be strongly depressed posteriorly in micheleids to enclose the midanterior sclerite of abdominal somite 1.

In the more shrimp-like forms abdominal somite 1 is half as long as the second, is sclerotised anterior to the anterolateral lobes, and possesses a prominent pleuron (fig. 7a). The anterior margin of the pleuron of abdominal somite 2 extends forward and covers the posterior margin of abdominal somite 1 (reptant- and caridean-like). Lateral condyles ensure that articulation between the first and second somites is in one plane.

In burrowing forms the cephalothorax-abdomen relationship is similar except that abdominal somite 2 is longer. Some species are more shrimp-like than others but there is a tendency for greater flexibility than in Axiidae, for example, by weakening of the lateral condyles. The pleuron of abdominal somite 1 is not prominent and is represented only by a non-projecting lateral plate. In callianassid-like genera the anterior sclerotisation is weak.

In the elongate burrowing families the anterolateral lobes on abdominal somite 1 and the posterolateral carapace ridges on which they ride in primitive forms are obsolete or absent. Abdominal somite 1 is elongate, almost or about as long as the second, and its pleuron obsolete. The anterior margin of abdominal pleuron 2 does not overlap anteriorly (figs 2b, 2c, 7e).

Characters 10–17 in Table 1 summarise evolutionary changes in the posterior carapace and abdominal somites 1 and 2.

Thoracic sternites. Thoracic sternite 7 is a complex structure which bears pereopods 4. In all thalassinideans, anomurans and in *Neoglyphea* it is separate from and more substantial than sternite 8 (character 18). Sakai and de Saint Laurent (1989) illustrated its variation in Axiidae but not very exactly in many cases. Homologies between the structures seen in Thalassinidea and in the other reptants are not clear. In *Neoglyphea* the articulation of coxa 4 is oblique on two condyles, and the sternite bears two sinuous episternal ridges which are well separate posteriorly (Forest and de Saint Laurent, 1989: fig. 2). In all thalassinideans the episternal ridges meet posteriorly where they are separated by a deep slit. There is a median ridge anterior to the coxal condyles (fig. 8a). There is a tendency in the burrowing forms for the episternal ridges to become obsolete posteriorly (the sternite to be smooth except for the median slit), for the anterior ridge to be broadened, and for the articulation between sternite and coxa to become weak (figs 8b, c). Rarely, for example in some apparently advanced thomassiniids, remnants of the hooks of the episternal ridges are seen. Coxa 4, more or less cylindrical in *Neoglyphea* and primitive thalassinideans, becomes flattened in the burrowers, especially with the development of an anteromedial lobe which may meet its pair medially.

Characters 19–24 in Table 1 explain changes in thoracic sternite 7 and coxa of pereopod 4.

Gills. The changes in shape of the elements of the gills and number of thoracic gills are complex.

In the non-thalassinidean reptants the epipods vary in form, the elements of the gills (podobranchs, arthrobranchs and pleurobranchs) are digitiform or lamellate and either regularly or irregularly arranged along a rachis. In anomurans and thalassinideans the gill elements are regularly arranged in pairs except in *Thalassina*

where the gill elements are irregular filaments (fig. 6m). Paired lamellae would seem to be a strong unifying feature of many families (figs 6n, o). In some species of *Upogebia* each paired lamella appears divided into two. Ngoc-Ho (1981) hypothesised that this was a derived condition, subdivision of a broad lamella into two filaments, and correlated this with more advanced conditions such as a dorsal tooth on the mandible and absence of epipod on maxilliped 1. She contrasted this with the antithetical view of de Saint Laurent and Le Loeuff (1979) who viewed the four filamentous elements as more plesiomorphic than two lamellate elements. My examination of the underlying structure of the gills and correlation with other characters supports Ngoc-Ho's interpretation.

The most plesiomorphic condition of the number of gills is shown in *Neoglyphea* whose numbers of gills are as follows (Forest and de Saint Laurent, 1975):

Thoracomere:	1	2	3	4	5	6	7	8
Pleurobranchs	-	-	-	-	1	1	1	1
Arthrobranchs	1	1	2	2	2	2	2	-
Podobranchs	-	1	1	1	1	1	1	-
Epipods	-	1	1	1	1	1	1	1

The tendency for loss of thoracic branchiae throughout the Thalassinidea shows considerable homeoplasy and losses of different gills are not correlated. The absence of arthrobranch 1 and the loss or reduction of pleurobranch 8 are the only apomorphies common to all thalassinideans. *Thalassina* is unique in possessing a second smaller arthrobranch on thoracic somite 2. Epipods are primitively foliaceous at least posteriorly but become linear or lost in more apomorphic taxa. The presence of only a rudimentary gill is treated as an apomorphy in the same way as its loss in this analysis. In some genera, e.g. *Michelea*, *Crosniera* and *Mictaxius*, species exist with fewer gills than shown in Table 2. The most plesiomorphic condition known for the genus is that scored. Table 1 lists the characters 25–31 describing gills. In the first analysis charcters were treated as ordered and in an alternative, as unordered.

Cephalon and mouthparts. Long setae on the epistome are not widespread within the Reptantia; their presence is considered apomorphic (character 32) but their occurrence is irregular.

The cylindrical articulating eyestalk with a terminal cornea is the ancestral condition within the Decapoda (figs 4a–c, n). A flattened eyestalk with dorsal cornea is apomorphic (figs 4f, i–k; character 33).

An elongate waisted first article on antenna 1 is a peculiarity of micheleids (fig. 4f; character 34). Article 3 is primitively longer than the first two in outgroups and its shortening is a feature of axiids and micheleids (figs 4a, f; character 35). A similar situation is seen is some ctenochelids.

A scaphocerite (exopod) attached to the distal border of article 2 of antenna 2 is common in reptants and well developed in many carideans. It is accompanied often by the possession of a strong terminal spine (parallel to the scaphocerite) on article 2 and usually a small mesiodistal spine on article 3 (fig. 4a). Absence of the scaphocerite and spines is assumed to be apomorphic (fig. 4j; character 36). In the plesiomorphic state the scaphocerite is much longer than wide (fig. 4b) but its apomorphic states include a reduced but articulating acicle about as long as wide (figs 4i, k; state 1) or loss (fig. 4j; state 2). The character was treated as ordered and unordered in alternate analyses.

The mandibular incisor plesiomorphically, i.e. in outgroups and in most thalassinideans, has an anterior truncate blade-like part and a posterior toothed margin; the pair are symmetrical. Alternate apomorphic states are toothed along all the cutting edge (character 37) and asymmetrical (character 38).

The scaphognathite (epipod of maxilla 2) of reptants primitively has two lobes directed distally (or anteriorly) and proximally (or posteriorly into the branchial chamber). The latter lobe tapers and is fringed with setae which are longer apically. This is similar to the condition seen in thalassinids and laomediids but in these two families the posterior setae are thickened. In some thalassinidean families a long seta (or 2 setae in rare cases) on an acute apex of the proximal lobe extends the full length of the branchial cavity and interacts with the pereopodal epipods (fig. 6a). This was first recognised as a feature of axiids, *Callianidea* and *Thomassinia* (de Saint Laurent, 1979a). The presence of the seta was used as a defining character of the Callianideidae s.l. by Kensley and Heard (1991) and so is treated here as a synapomorphic state (character 39). The number, position, length and fine structure of the setae in Laomediidae and *Thalassina* suggest that they are not homologous. In most families the proximal lobe of the scaphognathite is shortened, rounded, and evenly fringed with plumose setae; this is treated as an apomorphy (fig. 6b;

character 40). However, there is strong evidence from the presence of a single long seta on the larvae of anomurans (Van Dover et al., 1982) that this may be a plesiomorphy.

The endopod of maxilliped 1 is 2-articled or elongate in the plesiomorphic state (fig. 6c) and minute when apomorphic (character 41). Its exopod is flagellate when plesiomorphic (fig. 6c) and 1-articled and foliaceous when apomorphic (character 42). Loss of the exopod is also apomorphic (character 43).

The plesiomorphic reptant maxilliped 3 endopod is a linear limb with elongate distal articles, with a well-developed crista dentata on the upper face, and spines along the mesial edges of the coxa-carpus (especially the merus) (fig. 6d). There are several apomorphic conditions most of which are frequently homeoplasic. As the proximal articles of the maxillipedal endopod become more operculiform in some callianassids the distal articles become more compact (fig. 6h; character 44). The exopod may become reduced or absent (figs 6f–i, k; character 45). The crista dentata is primitively a strong toothed ridge (fig. 6d; character 46) which may become a row of obsolete teeth or absent. Mesial spines on the merus are plesiomorphic (figs 4d, e) and one spine is common; absence of spines is apomorphic (character 47). Not all genera are consistent in this feature and even in callianassids where the maxilliped is often operculiform isolated cases of meral spines are recorded.

There is strong homeoplasy between and within genera in the loss of spines and exopods and as a consequence these are not considered of great evolutionary significance.

Pereopods. Fusion of the basis and ischium of all five pereopods is characteristic of all reptants except Glypheidae and Astacidea (character 48). A character state defining all Thalassinidea is the possession of a dense row of long setae on the lower basis-propodus margin of at least pereopod 2 (fig. 5h; character 49). In some families similar rows are well developed on other limbs (e.g., pereopods 1–4 in Upogebiidae). The setae are weaker on more posterior limbs in other families and the polarity of their development beyond pereopod 2 is uncertain.

The plesiomorphic reptant carpus and propodus of pereopod 1 are subcylindrical in cross-section and there is progressive flattening through the nephropids and thalassinideans. Flattening, especially of the carpus, and development of ridges on the upper and lower margins of both articles facilitates overlap between the merus and carpus when the leg is retracted and must help in burrow maintenance (fig. 5b; character 50). Articulation between the carpus and propodus of the primitive reptant allows movement through almost a right angle in a horizontal plane complementing vertical movement at the ischium-carpus joint; in all thalassinideans and hermit crabs movement here is considerably restricted (character 51). Equal chelipeds are plesiomorphic and unequal chelipeds apomorphic (character 52) but this character seems homeoplasic. Loss of spines from the lower margin of merus is apomorphic (character 53). The chelate nature of pereopod 1 is an apomorphic state shared with many reptants (character 54). I agree with Ngoc-Ho (1981) rather than de Saint Laurent and Le Loeuff (1979) that the chelate form in upogebiids is more plesiomorphic than the subchelate form (figs 5e, f) but this makes no difference to the character scores.

Although the first three pairs of pereopods of *Neoglyphea* are essentially simple each limb has an incipient thumb and it is easy to see how the chelate limb seen in many reptant groups arose. The Scyllaridea are the only other reptant group without chelate limbs; most (Anomura and Eubrachyura) have only the first pair of pereopods chelate; the Astacidea and Stenopodidea, with the non-reptant Penaeidea, have three pairs chelate; and the Eryonidea have four pairs chelate (de Saint Laurent, 1979b). The Thalassinidea all have a chelate or subchelate pereopod 1 but are variable for pereopod 2. De Saint Laurent (1979a) united the Axiidae, Callianassidae and Callianideidae, in part, on the chelate nature of pereopod 2 (fig. 5h). The most parsimonious hypothesis is that this is derived from the simple limb condition (character 55). *Thalassina* has a subchelate pereopod 2 but this is considered an independent autapomorphy (fig. 1a). Martin and Abele's (1986) phylogenetic analysis of the Anomura (including Thalassinidea) treated the absence of a chelate pereopod 3 an apomorphy of Thalassinidea, Upogebiidae and Laomediidae. The character is considered plesiomorphic in this analysis so does not feature here. Shortening of the fixed finger relative to the dactylus of pereopod 2 in *Michelea*, *Callianidea* and *Tethisea* is a character state differentiating these genera from the remaining thalassinideans (character 56). A strong proximal lobe or 'heel' on the lower margin of the propodus of pereopod 3 (fig. 5n) is a feature uniting the callianassid genera (de Saint Laurent and Le Loeuff, 1979: fig. 14). It is one

of several characters uniting *Anacalliax* with the Callianassidae (character 57).

The presence of spiniform setae on distal articles of pereopods 3 and 4 is a feature of some thalassinidean genera but the homology and polarity of this character-suite is uncertain (fig. 5j, k). I assume that the acquisition of numerous spiniform setae is correlated with cryptic behaviour and that they have become lost in some burrowing forms. The numbers and position of spiniform setae vary considerably especially in the Axiidae and few characters are scored. The presence of spiniform setae on the dactylus of pereopods 3 and 4 is treated as an apomorphy (character 58). Similar spiniform setae in *Thalassina* and *Laomedia* are not considered homologous because of slight difference in position. Many axiid genera possess several rows of spiniform setae on the propodi of pereopods 3 and 4. Loss of these on pereopod 3 (character 59) and pereopod 4 (character 60) are apomorphies. In thomassiniids and callianideids a single spiniform seta on the lower margin of the propodus of pereopod 3 (fig. 5m; character 61) and of pereopod 4 (character 62) are treated as characters independent of the transverse rows of axiids and micheleids.

An apomorphy of the burrowing thalassinideans is broadening of pereopods 3 and 4 from a cylindrical to paddle shape (figs 5k–n; character 63). Pereopod 5 is short and able to be held closely posteriorly alongside abdominal somite 1 in thomassiniids and callianassids (character 64).

Body proportions. The ancestral reptant displays the typical caridoid facies, that is, the abdomen is strong and about as long as the cephalothorax, and the tail fan slightly reflexed to facilitate the reverse escape response. This body form is seen in *Neoglyphea*, upogebiids, laomediids and axiids (figs 1b, 1c, 3a). *Thalassina* is specialised only in having a narrow abdomen with narrow uropods (fig. 1a). In the burrowing forms the cephalothorax is a third or less of the total body length rather than half (character 65) but there is considerable variability. Elongation of the second abdominal somite relative to the first is a feature of micheleids (figs 3b, c; character 66) but there are some callianassid genera in which this abdominal somite is elongate. General flattening of the abdomen and loss of pleura accompanies elongation. This is most evident in some callianassids where abdominal somite 6 is especially flat and the lateral margin is a well defined setose ridge. Abdominal somites 3–5 or 3–6 are ornamented with dorsolateral dense tufts of plumose setae in some thalassinidean genera. This character is confined to the infraorder but polarity is uncertain (character 67).

Pleopods. Pleopods offer numerous characters for an understanding of the phylogeny of the Thalassinidea. The Callianassidae, with several genera (de Saint Laurent, 1979a; Manning and Felder, 1991, 1992; Manning, 1992; Rodrigues and Manning 1992) possess similar pleopods 3–5 and sexually dimorphic and diverse pleopods 1 and 2 (character 68). The endopods 3–5 are thickened, more or less triangular and, with the extended peduncles, meet along a straight mesial margin with their opposite pairs which are interlocked by means of appendices internae which are often minute (fig. 8k). The exopods are curved, foliaceous and envelope the endopods in such a way that each of the three pleopod pairs is a semicircular plate which could act as a ventilator in a narrow burrow. This condition is a synapomorphy for the family and is shared with *Anacalliax*. In all other Thalassinidea pleopods 2–5 are more or less similar and not modified in this way. The Calocarididae are also defined by a synapomorphic condition of pleopod 2: the endopod is not produced beyond the base of the complex appendix interna as it is in Axiidae (fig. 8g; Kensley, 1989).

In Axiidae, Calocarididae and Callianassidae subtle differences in the shape of the pleopods are useful generic characters but only more gross differences are useful at the family level.

The appendix interna on the inner margin of the pleopodal endopods is a feature of Glypheidae and all Thalassinidea except Thalassinidae, Laomediidae and Upogebiidae. The homology between curved hooks on male pleopod 1 and the same hooks on the elongate appendix interna of more posterior pleopods seems clear (Kensley, 1989). Because it was suspected that this might be a symplesiomorphy the presence of an appendix interna was not included in the analysis. A trial incorporating it as an apomorphy did not affect the resulting cladogram. Absence of the curved hooks on the male pleopod 1 in genera possessing an appendix interna on pleopods 2–5 is treated as an apomorphy (fig. 8d; character 69). In the Axiidae and related groups the second article of pleopod 1 is triangular (fig. 8d; character 70) with the minute hooks of the residual

appendix interna on the mesial angle. In laomediids, upogebiids and callianassids the male pleopod 1 is lost or minute (character 71).

The plesiomorphic appendix masculina is an elongate setose structure diverging from the appendix interna on male pleopod 2 (figs 8e, f). There is no evidence of it in *Upogebia* or *Laomedia* (character 73) and in some thomassiniids it is fused to the internal margin of the appendix interna (fig. 8i; character 72).

The burrowing way of life has lead to the development of auxiliary respiratory surfaces on the margins of pleopods 2–5. These take the form of marginal simple or branching cylindrical filaments in *Callianidea* (fig. 8m) or as flat lamellae in *Michelea* (fig. 8o). In spite of fundamental differences between the appearance of the auxiliary surfaces the first species of *Michelea* were described as members of *Callianidea*. The marginal extensions are not treated as homologues as done by Kensley and Heard (1991) and the characters are autapomorphies which do not appear in this analysis. Treating the presence of an auxiliary respiratory surface as a homologous character state (adding one character) made no difference to the cladogram. Two steps were added, one for each genus, suggesting that the filaments were independently derived.

Shape of the pleopodal rami may be useful at a generic level within the Axiidae but the strong lateral lobes (subtriangular shape) of exopods 2–5 of the micheleid genera link this group (fig. 8l; character 74).

Tail fan. The most frequently encountered shape for the uropodal rami is ovate (figs 7f, i). Loss of the exopodal suture seen in *Neoglyphea* and some axiids is considered apomorphic (fig. 7g–j; character 75). A dorsal thickening of the setose anterolateral margin of the uropodal exopod is a callianassid character shared with *Anacalliax* (fig. 7h; character 76); a notch on the margin of the exopod in *Mictaxius* is not considered homologous. In *Upogebia*, *Strahlaxius*, *Meticonaxius*, *Marcusiaxius* and *Tethisea* the distal margin of the endopod is straight and ends laterally in a definite angle (figs 7g, j, k; character 77). In these same genera the telson tends to be shorter than wide.

Primitively the telson and uropods bear dorsal spines often along the ribs (fig. 7f). Loss of spination is apomorphic (character 78).

In the primitive condition abdominal somite 6 carries a well developed epimeron produced ventrally to enclose the base of the pleopods; it has a marginal row of setae. In the more advanced thalassinideans the epimeron and its marginal setae are lost and the area is receptive to the horizontal folding forward of the tail fan (character 79).

Setal-rows. Setal-rows characterise many thalassinidean genera and are much more widespread systematically and morphologically than previously appreciated. Setal-rows were defined by (Kensley and Heard, 1991: figs 1, 2) as tight rows of short plumose setae, each seta in a pit-like structure. They occur in several places:

a longitudinal row near the rostral carina (if present);

one, two or three vertical rows on the anterolateral cephalothorax: marginally, at the base of the eyestalk; an intermediate row; and a row near the cervical groove (fig. 6l);

dorsolateral row on abdominal somite 1;

lateral row on all or some of abdominal somites 2–5;

three rows, a longitudinal row on the margin of the pleuron, a transverse row along the posterior dorsolateral margin, and an oblique row in between, on abdominal somite 6;

short transverse row on the mesial face of the propodus of pereopod 2;

one or two rows on the mesial face of the propodus of pereopods 3 and 4 (figs 5k, l).

No species has all setal-rows. For this reason I treat them as 14 independent characters in which the apomorphic state is acquisition of the setal-rows. Table 1 explains the plesiomorphic and apomorphic states assumed (characters 80 to 93).

Results

The cladogram (ordered characters)

The matrix of 27 taxa by 93 characters was treated to phylogenetic analysis in the program HENNIG86 version 1.5 using the *mhennig** and *bb** (extended branch-swapping) options to find the most parsimonious trees. The results were confirmed using the *global* and *mulpars* multiple branch-swapping options in PAUP 2.4. In the first analysis all characters were treated as ordered.

Four equally short trees of 240 steps, with consistency and retention indices (ci and ri) of 41 and 75 respectively, were obtained. Only two clades, each of three genera, could not be fully

dichotomously resolved. These were the genera of the Thomassiniidae and the three more advanced of the four genera of Micheleidae. These became resolved after successive weighting of the characters once with the *xs w* option in HENNIG86 to give a single fully dichotomous cladogram of the same length as the original four and with ci and ri of 63 and 87 respectively.

Weighting had the effect of removing nine characters, most of which reached their derived state independently in two or more genera or in small clades, and which would not intuitively be expected to define major taxa. Twenty-four characters (26%) retained ci and ri equal to 100 and are marked with * in Table 1. A further 31 characters (31%) had ci equal to 50, that is, changed from the plesiomorphic to apomorphic state only twice or reversed once.

The transformation series, apomorphic changes at all nodes of the cladogram, were investigated using the *apolist* option in PAUP 2.4 and with the program CLADOS. Ninety per cent of all steps in the cladogram were coincident in both transformation series but for 19 characters the nodes at which transformations took place were ambivalent. These were revealed with the *xs h* option in HENNIG86. The implication of this is that the state of 19 characters (in parentheses in Table 1) at some nodes was uncertain and they could not be used with certainty in defining supra-generic taxa. They are not included on fig. 9.

Character changes defining the clades and higher taxa

The cladogram derived using ordered characters resulted in several major clades for which taxonomic status exists or is proposed and which are discussed in detail. Clades are numbered as in fig. 9.

The Anomura and Thalassinidea (clade 51) share several apomorphies: possession of a linea thalassinica or linea anomurica (if considered homologous); free thoracic sternite 8; gill elements paired transversely along rachis; absence of podobranch 7; chelate or subchelate pereopod 1; and fused pereopodal basis–ischium. The cladogram suggests that the similar structure of the carpus–propodus joint of pereopod 1 may also be synapomorphic but convergence in thalassinideans and hermit crabs may be more probable. It is also hypothesised that the absence of a suture on the uropodal exopod is also a synapomorphy but this demands that the condition be reversed in some axiids and in Laomediidae.

Independent derivations of a linea thalassinica in non-axioid Thalassinidea and a linea anomurica in Anomura involve the same number of steps, two, as a single homologous structure lost in the axioids. Parsimony criteria cannot resolve this argument. Until it can be convincingly shown that there are fundamental structural differences between the linea anomurica and thalassinica which would support their independent evolution, I must assume their homology.

The synapomorphies of the Anomura (clade 29) are given in fig. 9 but are incomplete because this group was only an outgroup for this analysis. All are paralleled in the Thalassinidea.

The Thalassinidea (clade 50) share only a single synapomorphy which is never reversed, that is, a row of setae on the lower margin of ischium–propodus of pereopod 2. Other character changes are reversed in some genera or families: posterior margin of carapace with strong lateral lobes (lost in callianassoids); thoracic sternite 7, episternites contiguous posteriorly and flattened; and pleurobranchs absent (present in micheleids, some axiids and some upogebiids). A chelate pereopod 2 is a possible synapomorphy reversed partly in Thalassinidae and fully in Upogebiidae and Laomediidae.

Of the three clades here treated as superfamilies two, Thalassinoidea and Callianassoidea, are sister taxa (clade 49). Three clear character states define this clade: absence of medial rostral carina, reduced scaphocerite, and unarmed telson.

The first superfamily, Thalassinoidea, is represented by a single family and genus defined by numerous autapomorphies not included in this analysis and others which are convergent in other taxa: lateral ocular ridges on the rostrum; failure of the anterolateral margin of abdominal somite 2 to overlap somite 1; flattened coxa 4. The irregular and unique gill elements is a reversal.

The second superfamily, Callianassoidea (clade 48), is defined by one unquestionable synapomorphy: posterior margin of carapace soft and without ridges. Others are ambivalent. The reduced rostrum, unarmed and obtusely triangular (sometimes spike-like) and without lateral carinae, is seen in all families except Upogebiidae and may be independently derived in Laomediidae and the others (clade 46). However, the upogebiid rostrum is unique, not very similar to that of the axioids or of the thalassinids and may be an autapomorphy. Reduction or absence of the male pleopod 1 is a possible synapomorphy but this requires a reversal in Laomediidae.

The Callianassoidea comprise six groups at family level of which the Laomediidae and Upogebiidae are the least derived. Laomediidae are characterised by: thoracic sternite 7, episternites diverging posteriorly (reversal); podobranchs 3–7 present (reversal); absence of a meral spine on maxilliped 3; and uropodal exopod with a transverse suture.

Upogebiidae share numerous autapomorphies and, among the characters discussed here: the broad rostrum; appendix masculina absent; and uropodal endopod distally truncate.

The remaining callianassoids group strongly in successive clades 47 and 46. Clade 47 is defined by absence of anterolateral lobes on abdominal somite 1, reduction of epipods and podobranchs, and other character states which may be reversals. Clade 46 shares seven unambivalent character steps: coxa 4 flattened, with anteromesial lobe; eyestalk flattened; pereopod 1, carpus–propodus flattened, unequal; pereopods 3 and 4, propodus flattened; male pleopod 1, appendix interna absent; and abdominal somite 6 epimeron not ventrally produced. The derivation of a chelate pereopod 2 seems probable at this point.

Clade 46 supports two pairs of families: Ctenochelidae + Callianassidae (clade 42) and Callianideidae + Micheleidae (clade 38).

Ctenochelidae plus Callianassidae (clade 42) share: abdominal somite 1, tergite anterior to anterolateral lobes flexible; absence of epipod 3; and shortened cephalothorax. The three ctenochelid genera cluster paraphyletically and share only a cardiac prominence, a feature also seen in *Anacalliax* which has more callianassid characters.

Callianassidae (clade 39) are a well defined family which share: pereopod 3 propodus uniquely with heel on proximal corner of lower margin; pleopods 1 and 2 sexually modified, 3–5 uniquely similar and lamellar; male pleopod 2, appendix masculina absent; and uropodal exopod with unique anterodorsal setose thickening.

Callianideidae and Thomassiniidae (clade 38) are united on: coxa 4 immobile and with condyle obsolete; maxilla 2 scaphognathite with a long seta; pereopod 1, merus uniquely with convex lower margin; and pereopods 3 and 4, propodus uniquely with 1 spiniform seta distally on lower margin. The derivation of setal-rows on pereopods 2–4 and abdominal somites 1 and 6 may link these two families but they may have been derived independently in individual genera.

The Callianideidae, comprising only *Callianidea*, are defined most clearly on the autapomorphy of marginal pleopodal filaments. The most significant characters in the analysis are: loss of the condyle and overlap between abdominal somites 1 and 2; and loss of appendix masculina. *Callianidea typa* is the only callianassoid in which the linea thalassinica is completely absent and so resembles an axioid, but its presence in *C. laevicauda* reinforces the callianassoid affinities of the genus.

Clade 37 links the three genera of the Thomassiniidae which share three consistent characters: linea thalassinica displaced dorsally, ocular lobe substituted by branchiostegal sclerite; mid-dorsal tergite of abdominal somite 1 anteriorly depressed; and midanterior region of thoracic sternite 7 flattened and broadened (coxae secondarily separate). Other character states defining the family are: maxilliped 3 ischium–merus at least slightly broadened, carpus–dactylus compact (shorter than ischium–merus); its exopod reduced or absent; without crista dentata or meral spine; pereopod 5 short, compact and fitting into side of abdominal somite 1; carapace with at least one vertical setal-row; and abdominal somite 6 with one setal-row.

The relationships between the three thomassiniid genera were resolved by the cladogram only after character weighting.

The third superfamily, Axioidea (clade 45), is uniquely characterised by absence of the linea thalassinica. Although it may be argued that the axioids are not part of the anomuran-thalassinidean line on the grounds that there is no linea, there are so many other shared characters of gills, sternites and pereopods that this seems improbable. Other apomorphies of this group are: antenna 1 with article 3 only as long as article 2; and maxilla 2 scaphognathite with a long seta.

Five family-level clades are recognised within the Axioidea.

The first is Calocarididae (clade 8) which are best defined on the autapomorphic structure of the second male pleopods (Kensley, 1989). Continued recognition as a separate family is based on not sharing the synapomorphies of the Axiidae.

Remaining axioids (clade 44) share vestigial or absent podobranch 2, possibly loss or arthrobranch 2, and abdominal somite 6 with a setal row. These divide into Axiidae s.s. (clade 43) and Strahlaxiidae + Micheleidae (clade 35).

Two apomorphies define clade 43 containing the four genera of Axiidae: pereopods 3 and 4,

dactylus and pereopod 4, propodus with spiniform setae. Review of the literature supports the fact that spiniform setae are variously developed throughout the family and that the character is an axiid synapomorphy. These two characters are shared with *Michelea* (Micheleidae) but not with other axioids. Because so few axiid genera were included, the relationships between them are not explored.

Strahlaxiidae and Micheleidae (clade 35) are particularly strongly linked and two character states are unique: abdominal somite 2 is more than twice as long as abdominal somite 1; and the exopod of pleopods 2–5 is laterally lobed. Other important characters are: coxa 4 flattened, with anteromesial lobe; pereopods 3 and 4, propodus flattened (less than twice as long as wide); uropodal endopod distally truncate, distolateral margin subacute; and pereopods 2–4 and abdominal somites 1–6 with setal-rows.

Strahlaxiidae (clade 13) share: abdominal somites 3–5 with dense tufts of lateral setae (although this may be a plesiomorphic condition appearing irregularly in the Thalassinidea); male pleopod 1 without appendix interna; and appendix masculina absent. The three genera placed in this family share a bifid apex on the rostrum and rugose gastric region of the cephalothorax.

The four genera comprising the Micheleidae (clade 34) are characterised by four unique synapomorphies, seven other synapomorphies and one reversal. The unique synapomorphies are: antenna 1, article 1 elongate and waisted; mandibular incisor asymmetrical; longitudinal carinal setal-row; and 2–3 carapace vertical setal-rows. Other important characters are: rostrum unarmed; pereopod 1, carpus-propodus flattened; cephalothorax less than one third body length; and telson and uropod unarmed. The reversal is the presence of pleurobranchs 5–7 (or at least 7).

Tethisea is the most primitive of the micheleids; the rest (clade 33) share five synapomorphies of which a second setal-row on pereopods 3 and 4 is unique. *Michelea* is characterised by 16 character changes among the suite listed here (notably absence of rostrum) but the most significant defining character is its marginal pleopodal lamellae. The relationships between *Michelea*, *Marcusiaxius* and *Meticonaxius* were resolved in the cladogram only after character weighting.

An alternate cladogram (unordered charaters)

An alternate analysis was run with multistate characters 27, 29, 30, 31 and 36 unordered. Characters 27–31 deal with the numbers of epipods and branchiae and 36 with the scaphocerite. Making them unordered means that a change from any one state to any other is treated as one step, equal to a change between sequential states. The alternate analysis resulted in four equally parsimonious trees of 234 steps (ci = 42, ri = 75) which were fully resolved with successive weighting.

This differed from the one obtained using unordered characters, in: 1, being 6 steps shorter; 2, the relationships between the major clades; and 3, relationships between the thomassiniid genera. The shorter length was accounted for in the epipods (character 27 four steps shorter) and branchiae (characters 29–31 each one step shorter). Character 36 was one step longer. This cladogram suggested that *Thalassina* is the sister taxon to Axioidea rather than Callianassoidea. However, the supposed synapomorphies of *Thalassina* and Axioidea are largely ambivalent characters. The only unique synapomorphies are the chelate pereopod 2 and triangular male pleopod 1. The chelate pereopod 2 is of doubtful homology and occurs in higher Callianassoidea also. The same may be said of the second character. The rearrangement of the thomassiniid genera was obtained only after successive weighting and remains questionable.

Ambivalent characters

Typically, ambivalent characters are explained by the inability of the phylogenetic programs to choose between one apomorphic step and one reversal, on the one hand, and two independent apomorphic steps, on the other. Both contribute two steps to tree length. Independent steps, which imply that these characters are non-homologous, is the commonsense interpretation for many. Others are more difficult to interpret. Character 3, for example, the flattened and shortened rostrum could have evolved independently in the Laomediidae and the non-upogebiid callianassoids, or been derived once in the Callianassoidea. In the latter case the upogebiid rostrum is a new character, and its specialised structure suggests this may be possible. A chelate pereopod 2 is another character about which the analysis was doubtful. Assuming it is apomorphic, which itself is uncertain, this character state could have arisen independently in Axioidea and advanced Callianassoidea, or have been lost in laomediids and upogebiids independently. The former is the more likely scenario since the condition in *Thalassina* is quite different from in other thalassinideans.

A new classification of the Thalassinidea

The generally high values of ci and ri give considerable confidence in the structure of the cladograms and it is used to hypothesise a classification as follows (clade numbers in fig. 9 in brackets). The alternate cladograms derived using ordered and unordered characters differ only in the relationships of the superfamilies and genera in one family, neither discrepancy affecting the classification.

Infraorder Anomura (29)

Infraorder Thalassinidea (51)

Superfamily Thalassinoidea Dana, 1852 (6)
- Family Thalassinidae Dana, 1852 (6)

Superfamily Callianassoidea Dana, 1852 (48)
- Family Laomediidae Borradaile, 1903 (7)
- Family Upogebiidae Borradaile, 1903 (21)
- Family Callianideidae Kossmann, 1880 (22)
- Family Thomassiniidae de Saint Laurent, 1979a (37)
- Family Ctenochelidae Manning and Felder, 1991 (42, 41, 40)
- Family Callianassidae Dana, 1852 (39)

Superfamily Axioidea Huxley, 1879 (45)
- Family Calocarididae Ortmann, 1891 (8)
- Family Axiidae Huxley, 1879 (43)
- Family Strahlaxiidae fam. nov. (13)
- Family Micheleidae Sakai, 1992a (34)

The significant taxonomic changes proposed are:

1. Definition of the Thalassinidea as a monophyletic taxon distinct from the Anomura;
2. Division of the Thalassinidea into three monophyletic superfamilies;
3. Restriction of the Callianideidae to its type genus.
4. Confirmation and definition of the family groups Thomassiniidae and Micheleidae (incorporating Meticonaxiinae Sakai, 1992b).
5. Recognition of the Ctenochelidae as a paraphyletic family;
6. Erection of a new family, Strahlaxiidae.

Discussion

Although as many as 18 family-group taxa have been proposed for the Thalassinidea, their relationships are disputed. Discussion in the literature mostly concerns the similarities or differences between only two taxa (Callianassidae and Upogebiidae in particular). Few contributions have offered data on three or more taxa (necessary to resolve trees) and only recently have plesiomorphic and apomorphic similarities been distinguished.

The first synthetic work was that of Borradaile (1903) who recognised only four families: Axiidae, Laomediidae, Thalassinidae and Callianassidae. Most of the 23 genera and subgenera defined by him are still valid, the greatest divergences from present nomenclature being in the Callianassidae. Borradaile's tree of 'genealogical relations' is similar to that derived from my analysis; in fact, its basic dichotomies are identical. The tree and his key define one clade containing *Calocaris* and other axiid genera, and a second clade which splits off the Laomediidae, Thalassinidae, Upogebiidae, Callianideidae and Callianassidae in turn (as in my most parsimonious cladogram). The congruence between Borradaile's and my trees is remarkable especially given the greater number of taxa and characters used by me.

Borradaile's tree of generic and family relationships has not always been accepted.

Gurney (1938) tackled the problem of thalassinidean relationships by examining larval characters. He concluded that larval characters common to all thalassinideans are shared with the lobster *Homarus* but that the group is not homogenous. He recognised "two series of genera which might be regarded as Homarine and Anomuran respectively". In his tree the anomuran group (Upogebiidae and Laomediidae) are

more closely related to the Anomura than to the homarine group (Axiidae and Callianassidae). Five larval characters were used to separate the two groups and some adult characters added to distinguish the Callianassidae and Upogebiidae. Much of his argument is taken up with the differences just between these last two families about which there is no dispute; only the affinities of Upogebiidae and Laomediidae to Anomura are relevant to thalassinidean phylogeny. Whether these characters are synapomorphies or shared plesiomorphies was not debated by Gurney and by his own admission the 'character . . . on which the greatest stress has been laid as evidence of relation to Anomura . . . is disputable'. Gurney's (1938) tree of affinities, which is very different from that proposed here, was criticised by Konishi (1989) on the basis of data from larvae of more families.

Gurney's tree of relationships proposes that the Thalassinidea are not monophyletic, rather, that the Axiidae + Callianassidae are the sister-group to the Anomura + Upogebiidae + Laomediidae. Such an arrangement presumes, as in my hypothesis, that the linea (thalassinica or anomurica) is homologous and was lost in the Axiidae. It assumes that the characters shared by Upogebiidae and Callianassidae arose independently: anterolateral lobes on abdominal somite 1 lost; reduction of epipods and podobranchs; and that the upogebiid rostrum is a unique apomorphy.

De Saint Laurent (1973) supported the differences between Callianassidae and Upogebiidae by raising the latter to full family rank but her grouping of the Callianideinae into Callianassidae was provisional. She too appeared to suspect that the callianassids have some axiid affinities but then offered no new evidence. She was uncertain about the affinities of the Upogebiidae but suspected they are close to Thalassinidae and Laomediidae, which is the case in my hypothetical tree.

De Saint Laurent (1979a, and in less detail in 1979b and in de Saint Laurent and Le Loeuff, 1979) grouped the Axiidae, Callianassidae and Callianideidae, in a superfamily, Axioidea, (or section Axiidea) which was defined as follows: reptant decapods with the epistome partially exposed, without a thelycum in the female, with pereopods 1–5 having the basis and ischium fused, with pereopods 1 and 2 chelate, pereopod 3 simple, pereopod 4 simple or subchelate, pereopod 5 chelate or subchelate, pleopods usually with an appendix interna, and maxilliped 1 always with a foliaceous epipod (my translation).

Several of these characters are true for all thalassinideans but the 'axioid' families as defined by de Saint Laurent (1979a) were said to differ from all others (Upogebiidae, Laomediidae and Thalassinidae) in the shape of the anterior region of the carapace, structure of the limbs and in larval morphology.

The peculiarities of the anterior margin of the carapace of 'axioids' were not defined. The most significant feature of the limbs distinguishing this superfamily group is that pereopod 2 is fully chelate, a condition never seen in other thalassinideans and is the only apomorphy shared. My analysis would suggest that chelate pereopods 2 have arisen independently in Callianassidae + Ctenochelidae (+ Thalassinidae) and Axioidea. Given the frequency of chelate limbs in the decapods this would not be a surprise.

Larval characters uniting the superfamily were listed by Gurney (1938) but plesiomorphic and apomorphic similarities of axiids and callianassids were not distinguished by him nor by subsequent authors. Because larvae of so few species are known with certainty, such characters cannot be easily investigated (Konishi, 1989). He tabulated the main zoeal characters of the Axiidae, Callianassidae, Upogebiidae, Thalassinidae and Laomediidae. He did not attempt to define relationships beyond stating his belief that the Axiidae are "most primitive and plesiomorphic in general feature" and that the upogebiids and laomediids are not grouped as in Gurney's (1938) scheme.

De Saint Laurent (1979b; reiterated in de Saint Laurent and Le Loeuff, 1979) ranked the Upogebiidae in a distinct section of Thalassinidea, Gebiidea, with Laomediidae and Thalassinidae. This was mainly on the basis of a simple pereopod 2 and convergence of habitus from a fossorial way of life. She noted the similarity of upogebiid larvae to those of 'Dromiacea' and the special 'trachelifer' larvae of laomediids without seeming to support Gurney's anomuran line.

De Saint Laurent's classification is not supported by parsimony criteria. Rearrangement of clades in my cladogram according to her scheme added 11 steps to the shortest tree. Significant homeoplasies added were: loss of posterolateral lobes on the carapace three times, in *Thalassina*, *Laomedia* and in Axioidea; loss of anterolateral lobes on abdominal somite 1 twice, in *Upogebia* and most callianassoids; loss of scaphocerite in two major clades; loss of podobranchs 3–6 twice, in *Upogebia* and higher callianassoids; and loss

or armature on telson and uropod twice.

Ngoc-Ho (1981) demonstrated that the larvae of Laomediidae and of Upogebiidae could be divided into subgroups and discussed similarities between them and with adult Glypheidae. Her discussion did not offer an opinion on the position of these two families relative to other thalassinideans.

The first cladistic analysis of the Thalassinidea was that of Martin and Abele (1986) who used 54 characters in an analysis of 20 taxa in the 'Anomura'. The monophyly of their group of five thalassinidean families and of de Saint Laurent's (1979a) superfamily was not supported by the most parsimonious cladogram but they concluded that the Thalassinidea could be recognised in a slightly longer tree.

Martin and Abele (1986) defined the Thalassinidea on the basis of two apomorphies: absence of pleurobranchs on thoracic somites 5–7; and possession of fewer than 14 pairs of gills (podobranchs excluded). Neither of these conditions is in fact the most plesiomorphic state found in thalassinideans. They did not recognise the presence of a linea thalassinica, which might be thought to be diagnostic of the taxon, as an apomorphy but rather as a more plesiomorphic condition of the linea anomurica.

Their division of the families was first into Laomediidae + Axiidae which share reduced male pleopods and phyllobranchiate gills, both states which are widespread in other thalassinidean families. The second major clade, Thalassinidae + Upogebiidae + Callianassidae, shared uropodal rami without sutures. The first two of these were said to share a subchelate first pereopod. This is not so for most upogebiids and is probably not homologous in the two families. It is not surprising that with only four characters effectively distinguishing the families their tree is different from that presented here.

Kensley and Heard (1991) presented a cladistic analysis using PAUP of the Callianideidae, defined a priori as a family of 18 species in seven genera, united by the possession of rows of special plumose setae on the carapace, some abdominal somites, and the propodi of pereopods 2–4. Their analysis used Axiidae, Laomediidae and Callianassidae as outgroups; 21 characters were used. Their most parsimonious result (18 34-step trees which I have calculated from their data) did not resolve the relationships between *Callianassa*, *Crosniera*, *Mictaxius* and *Thomassinia*, demonstrated that these four together were the sister-group of *Callianidea*, and showed that all five were isolated from *Michelea*, *Marcusiaxius* and *Meticonaxius*. This result has some similarity to my phylogeny in that Callianideidae, Micheleidae and possibly Thomassiniidae appear monophyletic. The tree was dismissed by Kensley and Heard because 'the ingroup could not be rooted as monophyletic'. On the contrary, it demonstrates that on the basis of this small dataset the 'Callianideidae' s.l. are *not* monophyletic. In spite of this evidence Kensley and Heard (1991) insisted on the monophyly of their seven genera and removed *Callianassa* from the analysis. One effect of this was to reduce the number of informative characters to only 15. My calculation from their data produced two unresolved trees of 23 steps and I was not able to reproduce their cladograms (1991: fig. 25). However, some synapomorphies of each of the Callianideidae (s.s.), Micheleidae and Thomassiniidae are shown in spite of their interrelationships being misleading.

Kensley and Heard's (1991) revision and phylogenetic analysis of genera was accepted by Sakai (1992a) who recognised the callianassid affinities of the Thomassiniidae and the axiid affinities of the others. His 'cladogram' (Sakai, 1992a: fig. 1) was constructed in an unconventional manner in order to illustrate these affinities and is not based on phylogenetic principles. His opinion that the Thalassinidae are more closely related to the Callianideidae than to other families is not supported here. He noted that both groups have setal pits but their structure and positions differ.

There are two views of the relationship of the Calocarididae to the Axiidae. Sakai and de Saint Laurent (1989) and Sakai (1992b) did not recognise the family as distinct but Kensley's (1989) hypothetical scheme used three synapomorphies to separate its four genera from the Axiidae. My phylogeny supports this result and goes further in suggesting some synapomorphies for the other axiid-like genera.

The Strahlaxiidae have not been recognised as distinct before. *Strahlaxius* is a sister-group of the Micheleidae and the two families share several synapomorphies. It is their separation from the Axiidae which enables the new family to be recognised.

My analysis was not detailed enough to support or deny Manning and Felder's (1991) revision of the Callianassidae and introduction of the Ctenochelidae. For the time being, Ctenochelidae are recognised as a paraphyletic taxon. Its original diagnosis includes only two synapo-

morphies, a cardiac prominence and a uropodal exopod notch, neither present in all genera.

THALASSINIDEA Latreille

Diagnosis. Reptant decapods without a thelycum in the female; with pereopods 1–5 having the basis and ischium fused; with pereopod 1 chelate and carpus-propodus articulation slight; pereopod 2 chelate or simple; *always with dense row of long setae on lower margin*; pereopod 3 simple; pereopod 4 simple or subchelate; pereopod 5 chelate or subchelate; without arthrobranch on thoracomere 1.

Key to superfamilies and families of Thalassinidea

1. Linea thalassinica absent; antenna 1 with article 3 about as long as article 2 (fig. 4a) .... Axioidea. 2
— Linea thalassinica present at least anteriorly (figs 4j, l–n) (if absent, with flattened eyestalks and cylindrical pleopodal marginal filaments (fig. 4k)); antenna 1 with article 3 usually longer than 2 5
2. Pleopod 2 endopod simple, with terminal enlarged appendix masculina (fig. 8g); eye unpigmented; uropod exopod usually with suture .... Calocarididae
— Pleopod 2 endopod foliaceous with small appendix masculina attached mesially (figs 8e, l); eye usually pigmented; uropod exopod usually without suture 3
3. Abdominal somite 2 less than twice as long as 3; exopods of pleopods 2–5 not laterally lobed (fig. 8e); pleuron of abdominal somite 1 produced; coxa of pereopod 4 more or less cylindrical; propodus of pereopods 3 and 4 more or less linear; uropodal endopod ovate (fig. 7f); pereopods 2–4 and abdominal somites without setal-rows .... Axiidae
— Abdominal somite 2 twice as long as 3; exopods of pleopods 2–5 laterally lobed (fig. 8l); pleuron of abdominal somite 1 not produced; coxa of pereopod 4 flattened; propodus of pereopods 3 and 4 more or less flattened (figs 5k, l); uropodal endopod triangular or ovate (fig. 7g); some of pereopods 2–4 (figs 5k, l) and abdominal somites with setal-rows 4
4. Rostrum spinose, apically bifid (fig. 4d); longitudinal and vertical setal-rows on carapace absent; antenna 1, article 1 as long as 2; mandibular incisor toothed and symmetrical; epipods and podobranchs reduced posteriorly .... Strahlaxiidae
— Rostrum not spinose; longitudinal and vertical setal-rows on carapace present; antenna 1, article 1 longer than 2 (figs 4f, h); mandibular incisor not toothed and asymmetrical; epipods and podobranchs rarely reduced posteriorly .... Micheleidae
5. Uropodal rami linear; gill elements irregular, filamentous proximally and plate-like distally (fig. 6m); rostrum spinose, narrow .... Thalassinoidea
[1 family: Thalassinidae; 1 genus: *Thalassina* (fig. 1a). See Poore and Griffin, 1979 and Dworschak, 1992 for separation of the species]
— Uropodal rami lamellate; gill elements regularly paired, lamellate (fig. 6o); rostrum flat or obsolete .... Callianassoidea. . . 6
6. Posterior margin of carapace with lateral lobes (fig. 1b); abdominal somite 1 with anterolateral lobe; maxilla 2 scaphognathite with several long setae on posterior lobe .... Laomediidae
— Posterior margin of carapace evenly curved (fig. 2c); abdominal somite 1 without anterolateral lobes; maxilla 2 scaphognathite with 1 or without long seta on posterior lobe 7
7. Pereopods 1 equal; pereopod 2 simple (fig. 5i); rostrum usually broad and setose (figs 4n–r); eyestalks cylindrical; coxa of pereopod 4 cylindrical .... Upogebiidae

— Pereopods 1 unequal, rarely equal; pereopod 2 chelate (fig. 4h); rostrum obsolete; eyestalks flattened (figs 4i–m); coxa of pereopod 4 flattened (figs 8b, c) 8

8. Maxilla 2 scaphognathite with long posterior seta (fig. 6a); pereopod 1 merus with convex lower margin; pereopod 3 (and sometimes 4) propodus with single distal spiniform seta on lower margin (fig. 5m); pereopods 2–4 and abdominal somites usually with setal-rows (figs 5k, l); abdominal somite 1 strongly chitinised anteriorly; cephalothorax half as long as total length; coxa of pereopod 4 immobile 9

— Maxilla 2 scaphognathite without long posterior seta (fig. 6b); pereopod 1 merus with straight or spinous lower margin; pereopod 3 propodus without distal spiniform seta on lower margin; pereopods 2–4 and abdominal somites without setal-rows; abdominal somite 1 weakly chitinised anteriorly; cephalothorax third as long as total length; coxa of pereopod 4 mobile 10

9. Linea thalassinica absent or short; pleopods with marginal filaments (fig. 8n); abdominal somite 1 with anterodorsal dome (fig. 2a); thoracic sternite 7 narrow (fig. 8c).......... Callianideidae
[1 genus: *Callianidea* (fig. 2a), 2 described species]

— Linea thalassinica present lateral to eyestalks (figs 4i, j); pleopods without marginal filaments; abdominal somite 1 anteriorly depressed (fig. 2b); thoracic sternite 7 broad, coxae 4 separate .... Thomassiniidae

10. Pleopod 2 similar to pleopods 3–5, rami lanceolate; pereopod 3 propodus linear or weakly ovate; uropodal exopod simply ovate .... Ctenochelidae

— Pleopod 2 reduced, sexually modified; pleopods 3–5 with broad interacting rami (figs 8j, k); pereopod 3 propodus with proximal heel on lower margin (fig. 5n); uropodal exopod with secondary setose lobe (fig. 7h) .... Callianassidae

AXIOIDEA Huxley

not Axioidea sensu de Saint Laurent, 1979a: 1395.

Diagnosis. Thalassinidea. Posterior margin of carapace with lateral lobes; *linea thalassinica absent*; pleuron of abdominal somite 1 more or less produced; eyestalks cylindrical; antenna 1 with article 3 about as long as article 2; maxilla 2 scaphognathite with 1–2 long setae on posterior margin; gill elements paired; pereopod 2 chelate; *pleopods with appendix interna*; pleopod 2 similar to pleopods 3–5; uropodal rami lamellate.

Axiidae Huxley

Diagnosis. Axioidea. Rostrum usually spinose, *apically acute*; eye usually pigmented; pleuron of abdominal somite 1 produced; abdominal somite 2 less than twice as long as 3; propodus of pereopods 3 and 4 linear or broadened; coxa of pereopod 4 more or less cylindrical; male pleopod 2 endopod foliaceous with small appendix masculina attached mesially; exopods of pleopods 2–5 not laterally lobed; *uropodal endopod ovate*; pereopods 2–4 without setal-rows, abdominal somite 6 with longitudinal setal-row.

Key to genera of Axiidae

The most recent key to the genera of this family (Sakai and de Saint Laurent, 1989) did not take into account the removal of genera to Calocarididae or the new family, Strahlaxiidae. The manuscript was published independently by K. Sakai and contains many errors (M. de Saint Laurent, pers. comm.). I am extremely grateful to M. de Saint Laurent for pointing out and correcting the errors; these improvements have been incorporated in this revised but pragmatic key. Nevertheless, many

species still do not fit well with existing generic diagnoses and a reappraisal of the family is needed. Couplet 1 can be difficult if the uropodal exopod suture is obscure. If in doubt try the unusual genera leading from the first alternate before going to couplet 5.

1. Uropodal exopod without transverse suture (or suture obscure) 2
— Uropodal exopod with transverse suture (fig. 7a) (sometimes without) 5
2. Eyes weakly or not pigmented (rarely fully pigmented); rostrum level with carapace (fig. 4a) 3
— Eyes fully pigmented; rostrum significantly depressed below level of carapace (fig. 4c) 4
3. Pereopods 1 equal, fixed finger short; pleura of abdominal somites 3–5 posteriorly rounded .... *Anophthalmaxius* De Man, 1905
— Pereopods 1 unequal, fixed finger of smaller cheliped basally almost as broad as propodus (fig. 5g); pleura of abdominal somites 3–5 posteriorly angled................ *Eiconaxius* Bate, 1888
4. Male pleopod 1 present; median carina ends anteriorly in angle or tooth; submedian carinae present (fig. 4c) .... *Scytoleptus* Gerstaecker, 1856
— Male pleopod 1 absent; median carina rounded anteriorly; submedian carinae absent .... *Parascytoleptus* Sakai and de Saint Laurent, 1989
5. Pereopodal epipods absent (or vestigial on pereopods 4 and 5 only); rostrum a short acute spike; maxillipedal 3 exopod with clear bend (fig. 6e) .... Coralaxiinae . . . *Coralaxius* Kensley and Gore, 1981
— Pereopodal epipods present on 1–4 (fig. 6n); rostrum not a spike, usually broad, dentate, longer than eyes; maxillipedal 3 exopod not clearly bent (fig. 6d) 6
6. Pleopods 2–5 without appendix interna; antenna 2 scaphocerite usually bifurcate (fig. 4s) .... *Eutrichocheles* Wood Mason, 1876
— Pleopods 2–5 with appendix interna (fig. 8m); antenna 2 scaphocerite usually simple 7
7. Pleurobranchs 5–7 (above pereopods 2–4) present (absent in 1 undescribed species of *Spongiaxius*) 8
— Pleurobranchs 5–7 (above pereopods 2–4) absent 13
8. Supraocular spines absent, rostrum evenly and weakly dentate (fig. 4e) .... *Axius* Leach, 1815
— Supraocular spines present, i.e. basal rostral spine well developed, often larger than more distal spines (fig. 4b) 9
9. Male pleopod 1 present (sometimes absent in *Spongiaxius*)................10
— Male pleopod 1 absent 12
10. Antenna 2 scaphocerite short, comma-shaped in lateral view (fig. 4t); rostrum with lateral rows of several erect spines; living in sponges .... *Spongiaxius* Sakai and de Saint Laurent, 1989
— Antenna 2 scaphocerite as long as article 4; rostrum with 1 or 2 lateral spines only; not living in sponges 11
11. Eyes fully pigmented, rounded................ *Bouvieraxius* Sakai and de Saint Laurent, 1989
— Eyes weakly pigmented, anteriorly flattened................ *Levantocaris* Galil and Clark, 1993
12. Rostrum twice as long as eyestalks, not depressed, strongly dentate; carapace carinae armed; pereopod 1 spinose................ *Calaxius* Sakai and de Saint Laurent, 1989
— Rostrum little longer than eyestalks, depressed, not dentate; carapace carinae unarmed; pereopod 1 not spinose................ *Dorphinaxius* Sakai and de Saint Laurent, 1989

13. Antenna 2 scaphocerite rudimentary; eyes weakly pigmented; male pleopod 1 present .... *Paraxius* Bate, 1888
— Antenna 2 scaphocerite at least moderately long; eyes fully (rarely weakly or not) pigmented; male pleopod 1 absent (rarely present) 14
14. Carapace covered with scale-like tubercles; rostrum styliform, usually shorter than elongate eyestalks; pereopod 1 granulate, spinose on upper margins..*Oxyrhynchaxius* Parisi, 1917
— Carapace smooth or spinose; rostrum not styliform (if narrow, longer than eyestalks which are not more than twice as long as wide); pereopod 1 spinose on upper margins or not 15
15. Eyestalks short (not more than half as long as rostrum); eyes weakly or not pigmented .... *Calocarides* Wollebaek, 1908
— Eyestalks long (at least half as long as rostrum); eyes fully pigmented 16
16. Rostrum narrow and acute (fig. 4b); supraocular spines present; pereopod 1 elongate, propodus and dactylus spinose or strongly setose on upper and lateral surfaces .... *Acanthaxius* Sakai and de Saint Laurent, 1989
— Rostrum broadly triangular; supraocular spines absent; pereopod 1 stout, propodus and dactylus smooth 17
17. Eyestalks elongate; median, submedian and lateral carinae unarmed ridges .... *Axiorygma* Kensley and Simmons, 1988
— Eyestalks stout; median, submedian and lateral carinae tuberculate, dentate or absent 18
18. Carapace carinae absent, strong paired tubercles instead; rostrum as long as or shorter than eyestalks ....*Allaxius* Sakai and de Saint Laurent, 1989
— Submedian carinae appear as horse-shoe-shaped line of weak tubercles; rostrum as long as or longer than eyestalks .... *Axiopsis* Borradaile, 1903

Calocarididae Ortmann

Diagnosis. Axioidea. Rostrum usually spinose, apically acute; *eye usually not pigmented*; pleuron of abdominal somite 1 produced; abdominal somite 2 less than twice as long as 3; propodus of pereopods 3 and 4 more or less linear; coxa of pereopod 4 more or less cylindrical; *male pleopod 2 endopod simple, with terminal enlarged appendix masculina*; exopods of pleopods 2–5 not laterally lobed; uropodal endopod ovate; pereopods 2–4 and abdominal somites without setal-rows.

Key to genera of Calocarididae

See Kensley (1989) and Sakai and de Saint Laurent (1989) for diagnoses of the genera and species and an entry to the literature. This key is a reconciliation of both works and adds the later genus of Sakai (1992b).

1. Uropodal exopod without transverse suture; sexes separate but some individuals hermaphroditic .... *Eucalastacus* Sakai, 1992
— Uropodal exopod with transverse suture; hermaphroditic 2
2. Carapace with strong post-cervical carina 3
— Carapace without post-cervical carina 4
3. Eyes flattened, mesially contiguous .... *Calocaris* Bell, 1853
— Eyes rounded, not mesially contiguous .... *Lophaxius* Kensley, 1989
4. Male pleopod 2 endopod with appendix interna and appendix masculina free, with 2 mesial rows of simple setae .... *Calastacus* Faxon, 1893
— Male pleopod 2 endopod with appendix interna and appendix masculina fused, with 2 mesial rows of spiniform setae 5

5. Appendix masculina elongate; podobranchs and arthrobranchs well developed.................................... *Calaxiopsis* Sakai and de Saint Laurent, 1989
— Appendix masculina boot-shaped; podobranchs and arthrobranchs rudimentary.................................. *Ambiaxius* Sakai and de Saint Laurent, 1989

Micheleidae Sakai

Micheleinae Sakai, 1992: 18.
Meticonaxiinae Sakai, 1992: 19.

Diagnosis. Axioidea. Rostrum *flat or obsolete*; eye usually pigmented; *antenna 1, article 1 longer than article 2*; *pleuron of abdominal somite 1 obsolete*; abdominal somite 2 twice as long as 3; propodus of pereopods 3 and 4 more or less broadened; coxa of pereopod 4 *flattened*; male pleopod 2 endopod foliaceous with small appendix masculina attached mesially; *exopods of pleopods 2–5 laterally lobed*; uropodal endopod *ovate*; *carapace, pereopods 2–4 and abdominal somites with some setal-rows*.

Remarks. Sakai (1992) erected the callianideid subfamily Micheleinae for genera without a linea thalassinica, with anterolateral lobes on abdominal somite 1, with a long scaphocerite, subequal first pereopods, with a small rostrum, and with normal propodus on pereopod 4. His second subfamily, Meticonaxiidae, differed mainly on the presence of a rostrum and absence of pleopodal filaments. The phylogenetic analysis suggests that the meticonaxiids are polyphyletic and must therefore be synonymised with Micheleidae. The subfamily is not related to the Callianideidae and is here elevated to family rank.

Key to genera of Micheleidae

The family is intended to include the two subfamilies of Callianideidae, Micheleinae and Meticonaxiinae, erected by Sakai (1992a). Its four genera include species have been variously included in Axiidae, Callianassidae and Callianideidae.

1. Rostrum minute, triangular (fig. 4f); without pleurobranchs; pereopods 3 and 4 with lateral spiniform setae (fig. 5k) ....*Michelea* Kensley and Heard, 1991
— Rostrum prominent, flat (figs 4g, h); with pleurobranchs; pereopods 3 and 4 without lateral spiniform setae 2
2. Cheliped with thickened setae in gape (fig. 5d); abdominal somites 3–5 without setal-rows; uropodal endopod with anterior margin convex, ending by curving to rounded posterior margin .... *Tethisea* gen. nov.
— Cheliped without thickened setae in gape; abdominal somites 3–5 with setal-rows; uropodal endopod with straight anterior margin ending sharply (fig. 7j) 3
3. Eyes visible in dorsal view, rostrum narrow (fig. 4g); cheliped fixed finger with major tooth two-thirds way along; maxilliped 2 exopod reduced ....*Meticonaxius* De Man, 1905
— Eyes not visible in dorsal view, rostrum wide (fig. 4h); cheliped fixed finger with major tooth one-third way along; maxilliped 2 exopod long ....*Marcusiaxius* Rodrigues and Carvalho, 1972

Tethisea gen. nov.

Type species. *Tethisea indica*, sp. nov.

Diagnosis. Micheleidae. Rostrum prominent, flat. Pleurobranchs 5–8 present. Pereopods 3 and 4 without lateral spiniform setae. Cheliped with thickened setae in gape. Abdominal somites 3–5 without setal-rows. Uropodal endopod with anterior margin convex, ending by curving to rounded posterior margin.

Etymology. From Tethys, the ancient ocean, alluding to the known distribution of this genus, and *Isea*, Guérin-Méneville's original genus of callianideid.

Remarks. *Tethisea* is most similar to *Marcusiax-*

ius and *Meticonaxius* in the possession of a rostrum and of pleurobranchs. The most obvious differences are the absence of setal-rows on abdominal somites 3–5, the presence of specialised thickened setae in the gape of pereopod 1, and the more ovate shape of the uropodal endopod.

Tethisea indica sp. nov.

Material examined. Holotype. Mozambique (24°64'S [sic], 35°20'E), 165 m, Agassiz trawl, 18 Aug 1964 (IIOE program, *Anton Bruun* cruise 7, stn 371D), National Museum of Natural History, Washington (USNM) 243552 (female, cl. 5.3 mm).

Paratypes. Mozambique, Mayotte, NNE of Récif Nord (12°31'S, 45°02'E), 300–350 m, course organic sand, dredge, 30 Mar 1977 (BENTHEDI stn 72DS), Muséum National d'Histoire Naturelle, Paris (MNHN) Th-1219 (2 males cl. 5.5 and 4.5 mm, female cl. 5 mm).

La Réunion (21°03.6'S, 55°09'E), 412-460 m, sand, Sanders dredge, 8 Sep 1982 (Cruise MD32 stn DS178), MNHN Th-1221 (1 specimen); MNHN Th-1223 (1 specimen).

Indonesia, Makassar Strait (0°54.2'S, 119°28.7'E), 170 m, 6 Nov 1980, grab (CORINDON 2 stn 248), MNHN Th-1216 (male cl. 6.5 mm, female, cl. 7 mm).

New Caledonia, E of SE corner of main island (22°15.32'S, 167°15.4'E), 440 m, Waren dredge, 5 Sep 1985 (MUSORSTOM BIOCAL stn DW77), MNHN Th-1226 (5 specimens); Museum of Victoria, Melbourne (NMV) J13268 (1 specimen).

Diagnosis. Rostrum triangular, 1.5 times as long as broad at base of eyes; posterior setal-row of 3 setae only. Maxilliped 3 merus without mesial tooth; exopod minute.

Cheliped merus with 2 spines on lower margin. Uropodal endopod with anterior margin convex, ending by curving to rounded posterior margin, 1.3 times as long as wide; exopod with concave anterior margin, apically rounded, posterior margin broadly lobed, 1.7 times as long as wide. Telson as long as wide, tapering to rounded–truncate apex beyond constriction one-third way along.

Remarks. The species and another in the same new genus will be described and figured in more detail in a later paper.

Strahlaxiidae fam. nov.

Type genus. Strahlaxius Sakai and de Saint Laurent, 1989.

Diagnosis. Axioidea. Rostrum usually spinose, *apically bifid*; eye usually pigmented; *antenna 1, article 1 as long as article 2*; pleuron of abdominal somite 1 *not* produced; abdominal somite 2 twice as long as 3; propodus of pereopods 3 and 4 broadened; coxa of pereopod 4 more or less flattened; male pleopod 2 endopod foliaceous with small appendix masculina attached mesially; *exopods of pleopods 2–5 laterally lobed*; *uropodal endopod triangular*; *pereopods 2–4 and abdominal somites with some setal-rows.*

Composition. Neaxius Borradaile, 1903; *Neaxiopsis* Sakai and de Saint Laurent, 1989; *Strahlaxius* Sakai and de Saint Laurent, 1989.

Remarks. The three strahlaxiid genera are superficially similar to some members of the Axiidae where they have traditionally been placed. The most significant diagnostic characters are the acute outer angle of the uropodal endopod, the bifid rostrum, rugose gastric region of the carapace, broad pleopodal rami, and possession of some setal-rows on some pereopods and abdominal somites. Absence of the appendix masculina is a synapomorphy but this is shared with some axiid genera.

The recognition of Axiidae, Calocarididae and Strahlaxiidae among the genera previously assigned to Axiidae s.l. does not deny the possible existence of other monophyletic taxa within this group. Strong evidence for the monophyly of the Calocarididae was argued by Kensley (1989) and unique diagnostic features of the Coralaxiinae were presented by Sakai and de Saint Laurent (1989). The existence of neither clade excludes the other, contrary to Sakai's (1992b) view, and my hypothesis is the first to attempt to relate them.

Key to genera of Strahlaxiidae

1. Antenna 2 scaphocerite toothed; pleurobranchs 5–7 (above pereopods 2–4) present; telson with 2 transverse ridges .... *Neaxius* Borradaile, 1903
— Antenna 2 scaphocerite simple; pleurobranchs 5–7 (above pereopods 2–4) absent; telson dorsally smooth (fig. 7g) 2
2. Male pleopod 1 present ....*Strahlaxius* Sakai and de Saint Laurent, 1989
— Male pleopod 1 absent ....*Neaxiopsis* Sakai and de Saint Laurent, 1989

CALLIANASSOIDEA Dana

Diagnosis. Thalassinidea. *Posterior margin of carapace with or without lateral lobes*; *linea thalassinica present*; pleuron of abdominal somite 1 weak; eyestalks cylindrical or flattened; antenna 1 with article 3 as long as or longer than article 2; maxilla 2 scaphognathite with or without long seta on posterior margin; gill elements paired; pereopod 2 simple or chelate; pereopods 3 and 4 propodus with or without spiniform setae; pereopods 2–4 and abdominal somites sometimes with setal-rows; pleopods with or without appendix interna, reduced if present; pleopod 2 similar or dissimilar to pleopods 3–5; uropodal rami lamellate.

Callianassidae Dana

Diagnosis. Callianassoidea. *Linea thalassinica present, lateral to antennae*; posterior margin of carapace evenly curved, rarely with cardiac prominence; rostrum obsolete or a spike; eyestalks flattened, rarely cylindrical; maxilla 2 scaphognathite without long seta on posterior lobe; abdominal somite 1 without anterolateral lobes, weakly chitinised; pereopods 1 unequal or equal; pereopod 1 merus with straight or toothed lower margin; pereopod 2 chelate; pereopod 3 propodus without distal spiniform seta on lower margin, *with proximal heel on lower margin*; coxa of pereopod 4 flattened, mobile; thoracic sternite 7 narrow; *pleopod 2 different from pleopods 3–5, sexually modified; pleopods 3–5 with broad interacting rami*; *uropodal exopod with thickened anterodorsal setose margin*; only abdominal somite 6 with setal-rows.

Key to genera of Callianassidae

The genera of the Callianassidae are poorly understood. De Saint Laurent and Le Loeuff (1979) provided a key to genera from the eastern Atlantic. Manning and Felder (1991, 1992), Manning (1992) Rodrigues and Manning (1992) and Manning and Lemaitre (1993) briefly diagnosed all the genera and gave keys to American forms. Both the French and American authors summarised earlier contributions but it is difficult to reconcile their two systems. The key here is based on both schemes and should be used for practical purposes only. The key seems unlikely to work for many Indo-West Pacific species.

1. Maxillipedal 3 dactylus ovate (fig. 6f); carapace lacking dorsal oval 2
— Maxillipedal 3 dactylus slender, digitiform (figs 6h, i); carapace with dorsal oval (fig. 2c) 3
2. Chelipeds equal, similar .... *Eucalliax* Manning and Felder, 1991
— Chelipeds unequal, dissimilar .... *Calliax* de Saint Laurent, 1973
3. Pleopods 3–5 with digitiform appendices internae (fig. 8j) 4
Pleopods 3–5 with stubby appendices internae (fig.8k 5
4. Maxilliped 3 without exopod; eyes subterminal, lateral .... *Cheramus* Bate, 1888
— Maxilliped 3 with exopod (fig. 6j); eyes terminal, subglobular .... *Scallasis* Bate, 1888
5. Eyes globular, terminal on cylindrical eyestalk; maxillipedal 3 merus with denticulate distal border .... *Calliapagurops* de Saint Laurent, 1973
— Eyes flattened, subterminal on flattened eyestalk; maxillipedal 3 merus without denticulate distal border 6
6. Maxillipedal 3 propodus oval, as broad as long, twice as wide as dactylus (fig. 6i) 7
— Maxillipedal 3 propodus slender, longer than broad, at most slightly wider than dactylus (fig. 6h) 14

7. Abdomen with strong pattern formed by symmetrical grooves on somites 3–5; uropodal endopod curved, strap-shaped.. ....*Callichirus* Stimpson, 1866
— Abdomen without pattern formed by symmetrical grooves on somites 3–5; uropodal endopod not curved or strap-shaped 8
8. Maxilliped 3 with exopod (fig. 6j); antenna 1 peduncle longer and stouter than antenna 2 peduncle .... *Lepidophthalmus* Holmes, 1904
— Maxilliped 3 without exopod; antenna 1 peduncle not longer and stouter than antenna 2 peduncle 9
9. Rostral spine absent or weak; front not or weakly trispinose 10
— Rostral spine distinct and upturned; front strongly trispinose (fig. 4l) 12
10. Linea thalassinica incomplete, not reaching to posterior margin of carapace .... *Poti* Rodrigues and Manning, 1992
— Linea thalassinica complete, reaching to posterior margin of carapace 11
11. Uropodal endopod broader than long, flattened distally; posterior margin of telson rounded or slightly indented ....*Neocallichirus* Sakai, 1988
— Uropodal endopod longer than broad, tapering distally; posterior margin of telson strongly excavate .... *Sergio* Manning and Lemaitre, 1994
12. Cheliped carpus and propodus with 3 spines on upper margin; eye disc-shaped, dorsal, narrower than eyestalk .... *Glypturus* Stimpson, 1866
— Cheliped carpus and propodus with unarmed upper margin; eye subglobular, distal, as wide as eyestalk 13
13. Abdominal somite 2 about as long as abdominal somite 6; carapace shorter than 10 mm .... *Corallichirus* Manning, 1992
— Abdominal somite 2 about as long as abdominal somite 6 plus telson; carapace about 25 mm .... *Corallianassa* Manning, 1987
14. Maxilliped 3 slender, pediform (fig. 6f) 15
— Maxilliped 3 broad, operculiform (figs 6h, i)...16
15. Cheliped with hook on merus (fig. 5b); male pleopod 2 vestigial or absent ....*Callianassa* Leach, 1814
— Cheliped without hook on merus; male pleopod 2 present, biramous .... *Anacalliax* de Saint Laurent, 1973
16. Maxillipedal 3 merus strongly projecting beyond articulation with carpus (fig. 6h); antenna 1 peduncle longer and stouter than antenna 2 peduncle 17
— Maxillipedal 3 merus barely or not projecting beyond articulation with carpus (fig. 6i); antenna 1 peduncle shorter and narrower than antenna 2 peduncle 18
17. Pleopods 3–5 with appendices internae embedded in endopod.................. .... *Neotrypaea* Manning and Felder, 1991
— Pleopods 3-5 with appendices internae projecting from endopod.............. .... *Trypaea* Dana, 1852
18. Carapace with rostral spine; male pleopod 2 present................................ .... *Notiax* Manning and Felder, 1991
— Carapace without rostral spine; male pleopod 2 vestigial or absent 19
19. Antenna 1 peduncle longer and stouter than antenna 2 peduncle; telson shorter than long .... *Gilvossius* Manning and Felder, 1992
— Antenna 1 peduncle not longer and stouter than antenna 2 peduncle; telson as wide as long (fig. 7h) .... *Biffarius* Manning and Felder, 1991

Callianideidae Kossmann

Diagnosis. Callianassoidea. *Linea thalassinica absent or very short*; posterior margin of carapace evenly curved, abdominal somite 1 without anterolateral lobes; rostrum reduced; eyestalks flattened; maxilla 2 scaphognathite with 1 long seta on posterior lobe; *abdominal somite 1 with anterodorsal dome*; pereopods 1 unequal; pereopod 1 merus with convex lower margin; pereopod 2 chelate; pereopods 3 and 4 propodus with single distal spiniform seta on lower margin; pereopod 3 propodus ovate; coxa of pereopod 4 flattened, immobile; thoracic sternite 7 narrow; pleopod 2 similar to pleopods 3–5, rami lanceolate, *with marginal filaments*; uropodal exopod simply ovate; pereopods 2–4 and abdominal somites 1 and 6 with setal-rows.

Composition. One genus, *Callianidea* Kossmann, 1880; two species (Sakai, 1992a).

Ctenochelidae Manning and Felder

Diagnosis. Callianassoidea. *Linea thalassinica present, lateral to antennae*; posterior margin of carapace evenly curved, with cardiac prominence; rostrum obsolete or a spike; eyestalks flattened; maxilla 2 scaphognathite without long seta on posterior lobe; abdominal somite 1 without anterolateral lobes, weakly chitinised; pereopods 1 unequal; pereopod 1 merus with straight or toothed lower margin; pereopod 2 chelate; pereopod 3 propodus without distal spiniform seta on lower margin; pereopod 3 propodus linear or weakly ovate; coxa of pereopod 4 flattened, mobile; thoracic sternite 7 narrow; *pleopod 2 similar to pleopods 3–5, rami lanceolate*; uropodal exopod simply ovate; only abdominal somite 6 sometimes with setal-rows.

Key to genera of Ctenochelidae

The phylogenetic analysis suggested that Ctenochelidae are a paraphyletic family but its relationships will only be discovered with a more thorough investigation of its genera and those of the Callianassidae. *Anacalliax*, included by Manning and Felder (1991), is removed to Callianassidae. The key combines the characters used by de Saint Laurent and Le Loeuff (1979: 47) and Manning and Felder (1991).

1. Carapace with dorsal oval; abdominal somite 6 with lateral projections .... *Callianopsis* de Saint Laurent, 1973
— Carapace without dorsal oval; abdominal somite 6 without lateral projections 2
2. Abdominal somite 1 with well developed pleura; cheliped carpus with mesial hirsute triangular depression .... *Paracalliax* de Saint Laurent and Le Loeuff, 1979
— Abdominal somite 1 without pleura; cheliped carpus without mesial hirsute triangular depression 3
3. Larger cheliped with fingers at least twice as long as palm, with a comb of fine teeth (fig. 5c); smaller cheliped propodus not tapering; rostrum spikelike .... *Ctenocheles* Kishinouye, 1926
— Larger cheliped with fingers shorter than palm, without a comb of fine teeth; smaller cheliped propodus tapering; rostrum obsolete or triangular 4
4. Maxilliped 3 with exopod (fig. 6j); abdominal somite 6 without sharp lateral projections .... *Gourretia* de Saint Laurent, 1973
— Maxilliped 3 without exopod; abdominal somite 6 with sharp lateral projections .... *Dawsonius* Manning and Felder, 1991

Laomediidae Borradaile

Diagnosis. Callianassoidea. *Linea thalassinica present*; *posterior margin of carapace with lateral lobes, abdominal somite 1 with anterolateral lobes*; *rostrum minute*; eyestalks cylindrical; *maxilla 2 scaphognathite with several thickened setae on posterior lobe*; abdominal somite 1 chitinised; pereopods 1 equal; *pereopod 2 simple*; pereopods 3 and 4 propodus with few spiniform setae on lower margin; pereopod 3 propodus linear; coxa of pereopod 4 cylindrical; thoracic sternite 7 narrow; pleopod 2 similar to pleopods 3–5, rami lanceolate; pleopods without appendix interna; uropodal exopod ovate; pereopods 2–4 and abdominal somites without setal-rows.

Key to genera of Laomediidae

The key is derived from the table of Kensley and Heard (1990) who listed the recent literature.

1. Uropodal rami both without transverse suture .... *Axianassa* Schmitt, 1924
— One or both uropodal rami with transverse suture 2
2. Uropod with transverse suture on exopod only; pereopods 3 and 4 dactylus with corneous spiniform setae; maxilliped 3 without exopod .... *Laurentiella* Le Loeuff and Intès, 1974
— Uropod with transverse suture on both rami; pereopods 3 and 4 dactylus without corneous spiniform setae; maxilliped 3 with exopod 3
3. Pereopod 1 subchelate; pereopods 2 and 5 simple; antenna 2 scaphocerite well developed .... *Naushonia* Kingsley, 1897
— Pereopod 1 chelate; pereopods 2 and 5 subchelate; antenna 2 scaphocerite reduced 4
4. Pereopods 1 dissimilar; pereopods 2–5 with reduced exopods; antenna 1 article 4 and antenna 2 article 3 short .... *Laomedia* De Haan, 1849
— Pereopods 1 similar; pereopods 2–5 without exopods; antenna 1 article 4 and antenna 2 article 3 elongate .... *Jaxea* Nardo, 1847

Thomassiniidae de Saint Laurent

Diagnosis. Callianassoidea. *Linea thalassinica well developed, starting immediately lateral to eyes*; posterior margin of carapace evenly curved; rostrum minute or a spike; eyestalks flattened; maxilla 2 scaphognathite with 1 long seta on posterior lobe; abdominal somite 1 without anterolateral lobes; pereopods 1 unequal; pereopod 1 merus with convex lower margin; pereopod 2 chelate; pereopod 3 (and sometimes 4) propodus with single distal spiniform seta on lower margin; pereopod 3 propodus broad or ovate; coxa of pereopod 4 flattened, immobile; thoracic sternite 7 broad; pleopod 2 similar to pleopods 3–5, rami lanceolate; uropodal exopod simply ovate; carapace and abdominal somite 6 with setal-rows.

Key to genera of Thomassiniidae

The three genera included here have been previously included in Callianassidae and Callianideidae.

1. Maxilliped 3 with brush of stiff setae on ischium and merus (fig. 6k); uropodal endopod with transverse row of spiniform setae .... *Thomassinia* de Saint Laurent, 1979
— Maxilliped 3 without brush of stiff setae on ischium and merus; uropodal endopod without transverse row of spiniform setae 2
2. Rostrum spike-like (fig. 4i); maxillipedal 3 exopod as long as merus .... *Crosniera* Kensley and Heard, 1991
— Rostrum obsolete, maxillipedal 3 exopod vestigial or absent..................... .... *Mictaxius* Kensley and Heard, 1991

Upogebiidae Borradaile

Diagnosis. Callianassoidea. *Linea thalassinica present, diverse*; posterior margin of carapace evenly curved, abdominal somite 1 without anterolateral lobes; *rostrum usually broad, spinose and dorsally setose*; eyestalks cylindrical; maxilla 2 scaphognathite without long seta on posterior lobe; abdominal somite 1 chitinised; *pereopods 1 equal*; *pereopod 2 simple*; pereopods 3 and 4 propodus without spiniform setae on lower margin; pereopod 3 propodus linear; coxa of pereopod 4 cylindrical; thoracic sternite 7 narrow; pleopod 2 similar to pleopods 3–5, rami lanceolate; pleopods without appendix interna; uropodal exopod triangular; pereopods 2–4 and abdominal somites without setal-rows.

Key to genera of Upogebiidae

The genera of the Upogebiidae are in flux and have not been analysed phylogenetically. This key summarises the recent contributions of Sakai (1982, 1993), Williams (1986), Ngoc-Ho (1989) and Williams and Ngoc-Ho (1990). *Gebicula* Alcock, 1901 is a senior subjective synonym of *Wolffogebia* Sakai, 1982. The subgenera *Calliadne* Strahl, 1862 and *Gebiopsis* Milne Edwards, 1868 are not in current usage but are available names.

1. Rostrum with 1 or more inferior spines (fig. 4n); distal margin of telson more or less concave; pereopod 1 subchelate, fixed finger short and spine-like, carpus and propodus with rows of strong spines on mesial and upper surfaces; uropodal exopod longer than telson .... *Gebiacantha* Ngoc-Ho, 1989

— Rostrum rarely with inferior spines; distal margin of telson usually convex; pereopod 1 chelate or subchelate (figs 5e, f), carpus and propodus smooth or with spines on upper surface; uropodal exopod rarely longer than telson 2

2. Anterior dorsal region of carapace and rostrum with scattered large yellow tubercles, lateral processes not differentiated from rostrum (fig. 4r) .... *Tuerkayogebia* Sakai, 1982

— Anterior dorsal region of carapace and rostrum usually with spines and/or setae, not tubercles, lateral processes differentiated or not (figs 4o-q) 3

3. Telson and uropods operculiform (fig. 7l).. .... *Pomatogebia* Williams and Ngoc-Ho, 1990

— Telson and uropods not operculiform (fig. 7k) 4

4. Anterior dorsal median region of carapace with low carina, without spines or setae (fig. 4o); pereopod 1 subchelate (fig. 5f) ....*Gebicula* Alcock, 1901

— Anterior dorsal median region of carapace with clear or obsolete furrow, with spines or setae (fig. 4p); pereopod 1 subchelate or chelate 5

5. Pereopod 1 simple, its dactylus without defined upper exterior plate; uropodal rami slender and leaf-like .... *Neogebicula* Sakai, 1982

— Pereopod 1 chelate (fig. 5e) or subchelate (fig. 5f), its dactylus with defined upper exterior plate; uropodal rami broad (fig. 7k) 6

6. Rostrum broadly separate from lateral crests (notch about as broad and deep as rostrum; fig. 4q); maxilliped 3 with crista dentata; maxilliped 2 dactylus subterminal; maxillipeds 2 and 3 exopods with 2-articled flagela .... *Acutigebia* Sakai, 1982

— Rostrum narrowly or only shallowly separate from lateral crests (notch usually narrower than rostrum; fig. 4p); maxilliped 3 with simple ischial hook, without crista dentata; maxilliped 2 dactylus terminal; maxillipeds 2 and 3 exopods with multiarticulate flagella ....*Upogebia* [Leach, 1814]

THALASSINOIDEA Dana

Diagnosis. Thalassinidea. Posterior margin of carapace with lateral lobes; linea thalassinica present; pleuron of abdominal somite 1 produced; eyestalks cylindrical; antenna 1 with article 3 about as long as article 2; maxilla 2 scaphognathite with thickened setae on posterior margin; *gill elements irregular, filamentous proximally and plate-like distally*; *pereopods 1 and 2 subchelate*; pereopods 3 and 4 propodus with spiniform seta; pereopods 2–4 and abdominal somites without setal-rows; pleopods 3–5 without appendix interna (vestigial on male pleopod 2); pleopod 2 similar to pleopods 3–5; *uropodal rami linear.*

Remarks. There is one family, Thalassinidae, with one genus, *Thalassina*. See Poore and Griffin, 1979 and Dworschak, 1992 for separation of the species. Sakai (1992a) described *T. anomala* in detail.

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Table 1. Character transformations used in the phylogenetic analysis of 22 taxa of Thalassinidea. Each character is numbered and described, the plesiomorphic state is followed by (0), and apomorphic states by (1) or for multiple state characters by higher numbers. Characters with consistency indices and retention indices of 100% after weighting by HENNIG86 are marked with *. Characters with ambivalent states at 2 or more nodes are in parentheses and are not included in fig. 9.

Carapace, linea thalassinica and rostrum

1.* Linea thalassinica or linea anomurica: absent (0); present (1).
2.* Linea thalassinica: typical (0); displaced dorsally, ocular lobes substituted by branchiostegal sclerite (1).
(3). Rostrum: longer than and covering eyestalks (0); reduced and obtusely triangular (sometimes spike-like) (1).
(4). Rostrum: flattened (0); spike-like (1).
5. Rostrum: spinose laterally (0); without armature (1).
6. Rostrum: simple (0); augmented by lateral ocular ridges (1).
7. Lateral carinae: present, with longitudinal row of setae (0); absent (1).
8. Medial rostral carina: present (0); absent (1).
9. Cardiac prominence: absent (0); present (1).

Carapace–abdomen articulation

10. Posterior margin of carapace: evenly convex (0); with strong lateral lobes (1).
11.* Abdominal somite 1 anterolateral lobes: present or indicated (0); absent (1).
12. Lateral articulation between abdominal somites 1 and 2: condyle present (0); condyle absent (1).
13. Posterior margin of carapace: ridged (0); soft, without ridges (1).
14.* Abdominal somite 1, tergite anterior to anterolateral lobes or their remnants: present and chitinised (0); absent, region flexible (1).
(15). Abdominal somite 1 pleuron: acute and projecting (0); blunt and obsolete (1).
16.* Abdominal somite 1 mid-dorsal tergite: anterior and posterior regions separate (0); regions amalgamated, anteriorly depressed (1).
17. Anterolateral margin of abdominal somite 2: overlaps abdominal somite 1 (0); does not overlap (1).

Thoracic sternites

18.* Thoracic sternite 8: fused to sternite 7 (0); free from sternite 7 (1).
19. Thoracic sternite 7, episternites: diverging posteriorly (0); contiguous posteriorly (1).
20. Thoracic sternite 7, episternites: acute (0); flattened (1).
21. Coxa of pereopod 4 posterior condyle: functional (0); obsolete or absent (1).
22. Coxa of pereopod 4: rectangular, without anteromesial lobe (0); flattened, with anteromesial lobe (1).
23. Coxa 4: mobile (0); immobile (1).
24.* Thoracic sternite 7, midanterior region: sharply ridged (0); flattened and broadened (coxae secondarily separate) (1).

Gills

25. Gill elements: irregularly arranged along rachis (0); paired transversely along rachis (1).
26. Epipods: broadly laminar (0); linear anteriorly and lost posteriorly (1).
(27). Epipods: 1–7 (rarely 2–7) present (0); 7 rudimentary or absent (1); 4–7 vestigial or absent (2); 3–7 absent (3); 2–7 absent (4).
(28). Podobranch 2: present (0); vestigial or absent (1).
29. Podobranchs 3–7: present (0); 7 absent (1); 3–7 absent or some rudimentary (2).
(30). Arthrobranchs on somites 1–7: 1122222 (0); 0122222 (1); 0022222 (2).
31. Pleurobranchs: 5–8 present (0); 5–7 (or rarely only 7) present, 8 rudimentary or absent (1); 5–8 absent (2).

Cephalon

(32). Epistome: without setae (0); with long setae (1).
33. Eyestalk: cylindrical, cornea terminal (0); flattened, cornea dorsal (1).
34.* Antenna 1, article 1: about as long as article 2 (0); elongate, waisted (1).
35. Antenna 1, article 3: longer than article 2 (0); as long as article 2 (1).
36. Antenna 2 scaphocerite: prominent, much longer than wide (0); reduced but articulating, about as long as wide (1); absent (2).
(37). Mandibular incisor: smooth anteriorly, denticulate posteriorly (0); toothed anteriorly and posteriorly (1).
38.* Mandibular incisor: symmetrical (0); asymetrical (1).
39. Maxilla 2 scaphognathite: without a long seta (0); with a long seta (1).
(40). Maxilla 2 scaphognathite, posterior lobe: tapering (0); rounded and evenly setose (1).
41. Maxilliped 1 endopod: 2-articled (or elongate and tapering) (0); minute (1).
(42). Maxilliped 1 exopod: 2-articled (with flagellum) (0); 1-articled (1).
43. Maxilliped 2 exopod: almost reaching to end of merus (0); reduced or absent (1).
44. Maxilliped 3: ischium–merus linear, carpus–dactylus linear (at least 6 times as long as wide) (0); ischium–merus at least slightly

broadened, carpus–dactylus compact (shorter than ischium–merus) (1).

(45). Maxilliped 3, exopod: reaching almost to end of merus (0); reduced or absent (1).

46. Maxilliped 3, crista dentata: prominent toothed ridge (0); obsolete or absent (1).

47. Maxilliped 3, meral spine: present (0); absent (1).

Pereopods

48.* Pereopodal basis — ischium: free (0); fused (1).

49.* Row of setae on lower margin of ischium — propodus of pereopod 2: absent (0); present (1).

50. Pereopod 1, carpus — propodus: cylindrical (0); flattened with upper and lower ridges (1).

(51). Pereopod 1, carpus — propodus: bending near right angles in horizontal plane (0); scarcely bending (1).

52.* Pereopod 1: equal (0); unequal (1).

53.* Pereopod 1, merus: with straight lower margin (0); with convex lower margin (1).

54.* Pereopod 1: simple (0); chelate or subchelate (1).

(55). Pereopod 2: simple (0); chelate (1).

56. Pereopod 2 dactylus: as long as fixed finger (0); longer than fixed finger (1).

57.* Pereopod 3 propodus: linear or oval (0); with heel on proximal corner of lower margin (1).

58. Pereopods 3 and 4, dactylus: without spiniform setae (0); with spiniform setae (1).

59. Pereopod 3, propodus: without spiniform setae (0); with rows of lower lateral spiniform setae (1).

60. Pereopod 4, propodus: without spiniform setae (0); with rows of lower lateral spiniform setae (1); with 1 spiniform seta distally on lower margin (2).

61.* Pereopod 3, propodus: without spiniform setae (0); with 1 spiniform seta distally on lower margin (1).

(62). Pereopod 4 propodus: without spiniform setae (0); with 1 spiniform seta distally on lower margin (1).

63. Pereopods 3 and 4, propodus: linear (on pereopod 3 more than 3 times as long as wide) (0); flattened (less than twice as long as wide) (1).

64. Pereopod 5: long and slender (0); short, compact and fitting into side of abdominal somite 1 (1).

Body proportions

65. Relative length of cephalothorax (cl/tl): half (0); third or less (1).

66.* Relative length of abdominal somite 2 to abdominal somite 1: less than 1.5 (0); more than 2 (1).

67. Abdominal somites 3–5: without setae laterally or at most sparse vertical rows (0); with dense tufts of lateral setae (1).

Pleopods

68.* Pleopods: 1 reduced, 2–5 similar and lamellar (0); 1 and 2 sexually modified, 3–5 similar and lamellar (1).

69. Male pleopod 1, appendix interna: present as minute hooks on ramus (0); absent (1).

(70). Male pleopod 1, second article: ovate (0); more or less triangular (1).

(71). Male pleopod 1: 1- or 2-articulate (0); minute or lost (1).

72.* Male pleopod 2, appendix masculina: present, prominent (0); fused to appendix interna (1).

73. Male pleopod 2, appendix masculina: present, prominent (0); absent (1).

74.* Pleopods 2–5 exopod: symmetrical (0); laterally lobed (1).

Tail fan

(75). Uropodal exopod: with transverse suture (0); without suture (1).

76.* Uropodal exopod: simply ovate (0); with anterodorsal setose thickening (1).

77. Uropodal endopod: distally rounded (0); distally truncate, distolateral margin subacute (1).

78. Telson and uropodal rami: with spines on surface (0); unarmed (1).

79. Abdominal somite 6 epimeron: ventrally produced, with mesial setae (0); not ventrally produced, without setae (1).

Setal-rows

80.* Longitudinal carinal setal-row: absent (0); present (1).

(81). Carapace vertical setal-row: absent (0); at least one present (1).

82.* Carapace vertical setal-rows: 1 present (0); 2 or 3 present (1).

(83). Pereopod 2 setal-row: absent (0); present (1).

(84). Pereopod 3 setal-rows: absent (0); 1 row present (1).

85.* Pereopod 3 setal-rows: 1 row only (0); second row present (1).

(86). Pereopod 4 setal-rows: absent (0); 1 row present (1).

87.* Pereopod 4 setal-rows: 1 row only (0); second row present (1).

88. Abdominal somite 1 setal-row: absent (0); present (1).

89. Abdominal somite 2 setal-row: absent (0); present (1).

90. Abdominal somites 3–5 setal-rows: absent (0); present (1).

91. Abdominal somite 6 longitudinal pleural setal-row: absent (0); present (1).

92. Abdominal somite 6, posterior setal-row: absent (0); present (1).

93. Abdominal somite 6, intermediate setal-row: absent (0); present (1).

Table 2. Genus-character matrix (27 genera by 93 characters) used in the HENNIG86 cladistic analysis of genera of the Thalassinidea. The first five taxa are outgroups. Unknown character states are shown by ?

	0	1	2	3	4	5	6	7	8	9
Neoglyphea	0000000000	0000000100	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	000
Enoplometopus	0000001000	0000000000	0000000002	0000000000	0000000000	0000000000	0000000001	0000000000	0000000000	000
Nephropsis	0000000000	0000000000	0000000002	0000000000	0000000000	0000000000	0000000000	0010000000	0000000000	000
Dardanus	1000000000	0000000100	0000111120	0000000000	0000000100	1001000000	0000000000	0000100000	0000000000	000
Munida	1000000000	0000000100	0000111120	0000000000	0000000100	0001000000	0000000000	0000100000	0000000000	000
Calocaris	0000000001	0000000111	0000100011	2000100010	0000000110	1001100000	0000000001	0000000000	0000000000	000
Coralaxius	0000000001	0000000111	0000102122	2000100010	0000000110	1001100111	0000000001	0000000000	0000000000	000
Axius	0000000001	0000000110	0000100011	1000100010	0000000110	1001100101	0000000001	0000000000	0000000000	010
Axiopsis	0000000001	0000000110	0000100012	2000100010	0000000110	1001100101	0000000001	0000000000	0000000000	010
Spongiaxius	0000000001	0000000111	0000100112	2000100010	0000000111	1001100111	0000000001	0000000000	0000000000	010
Strahlaxius	0000000001	0000100111	0100100112	2000100010	0000000110	1001100000	0010011010	0011101000	0011010110	011
Tethisea	0000100001	0000100111	0100100112	1001100110	0000100111	1001110000	0010110001	0001101111	1111010110	111
Marcusiaxius	0000100001	0000100111	0100100112	1101100110	0100111111	1001100000	0010110001	0001101111	1111111111	110
Meticonaxius	0000100001	0000100111	0100100112	1101100110	0110100111	1001100000	0010110001	0001101111	1111111111	111
Michelea	0010101101	0000100111	1110100122	1101110110	1010000111	1001110111	0010111001	0001101111	1111111111	011
Thalassina	1000010101	0000001111	0100000011	2000011000	0000000110	1001100000	0000000001	0000100100	0000000000	000
Laomedia	1010101101	0010000101	0000100001	2000011000	0000001110	1001000000	0000000000	1000000100	0000000000	000
Upogebia	1000011100	1010000111	0000112122	2000010001	0000000110	1001000000	0000000000	1010101100	0000000000	000
Callianidea	1010101100	1100101111	1110100122	2010010010	0100000111	1111110000	1110001010	0010100110	0011010100	010
Mictaxius	1110101100	1010110111	1111111121	2100011010	0101111111	1111100000	1111001010	0000100110	1011010111	011
Thomassinia	1110101100	1010110111	1111111122	2110021010	0101111111	1111100000	1011000010	0100100110	1000000100	111
Crosniera	1111101100	1010110111	1111110122	2110011010	0001010111	1111100000	1011001010	0100100110	1000000100	111
Paracalliax	1010101110	1011000111	0100113121	2110010001	0100000111	1101100000	00101000??	00?0100110	0000000000	000
Ctenocheles	1011101010	1111101111	0100114121	2110110001	0110100111	1101100000	0011100010	0000100110	1000000000	000
Gourretia	1011101110	1111101111	0100113121	2110110001	0101001111	1101100000	0011100010	0000100110	1000000000	111
Anacalliax	1010101010	1111101111	0100114122	2110110001	0001101111	1101101000	0001101110	0010110000	0000000100	111
Callianassa	1010101100	1111101111	0100113121	2110020001	1101101111	1101101000	0011101110	1010110110	0000000000	111

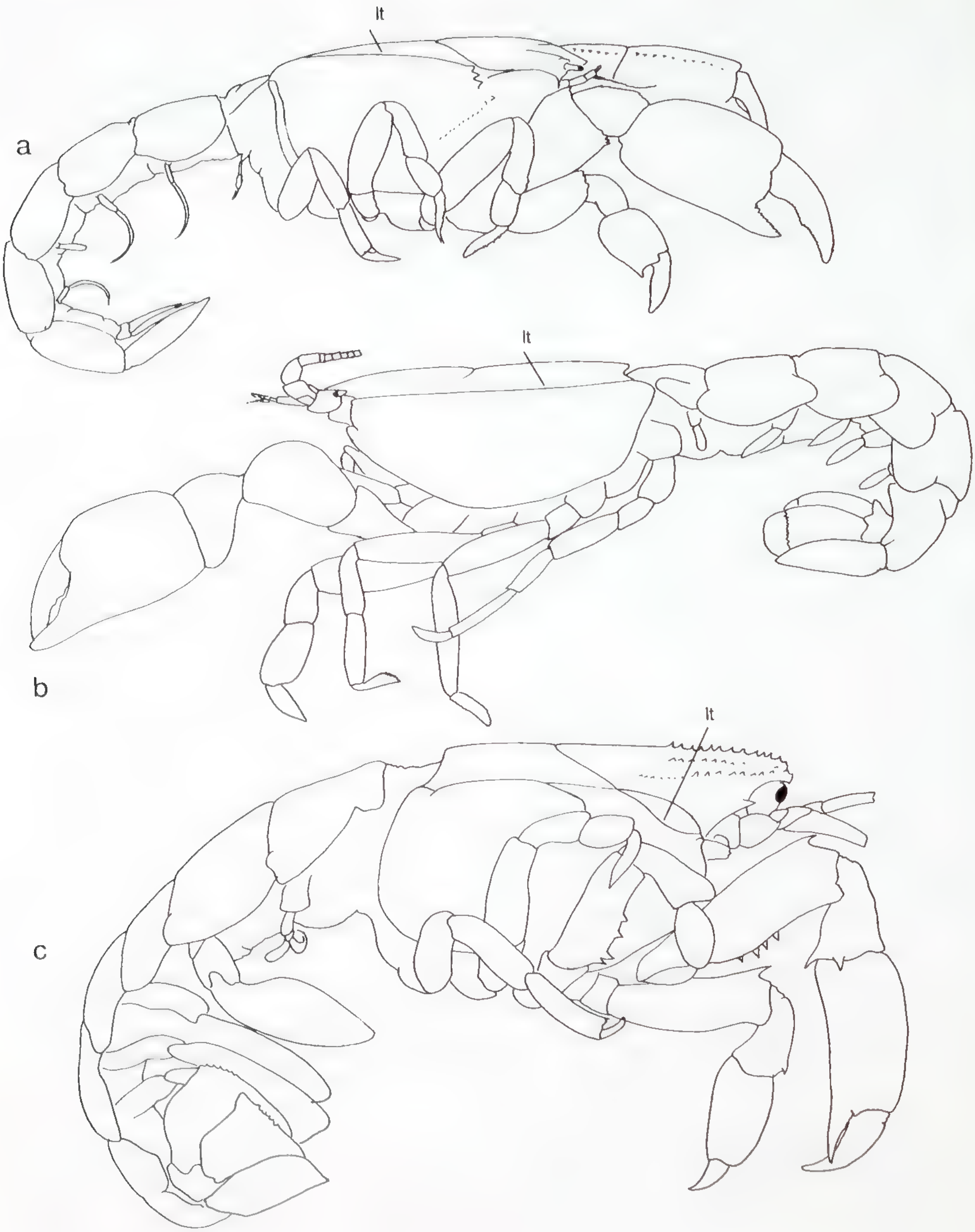


Figure 1. a, *Thalassina anomala* Herbst (Thalassinidae) [after Sakai, 1992a]; b, *Laomedia healyi* Yaldwyn and Wear (Laomediidae) [after Yaldwyn and Wear, 1972]; c, *Upogebia* species indeterminate (Upogebiidae) [after Williams, 1986].
lt = linea thalassinica.

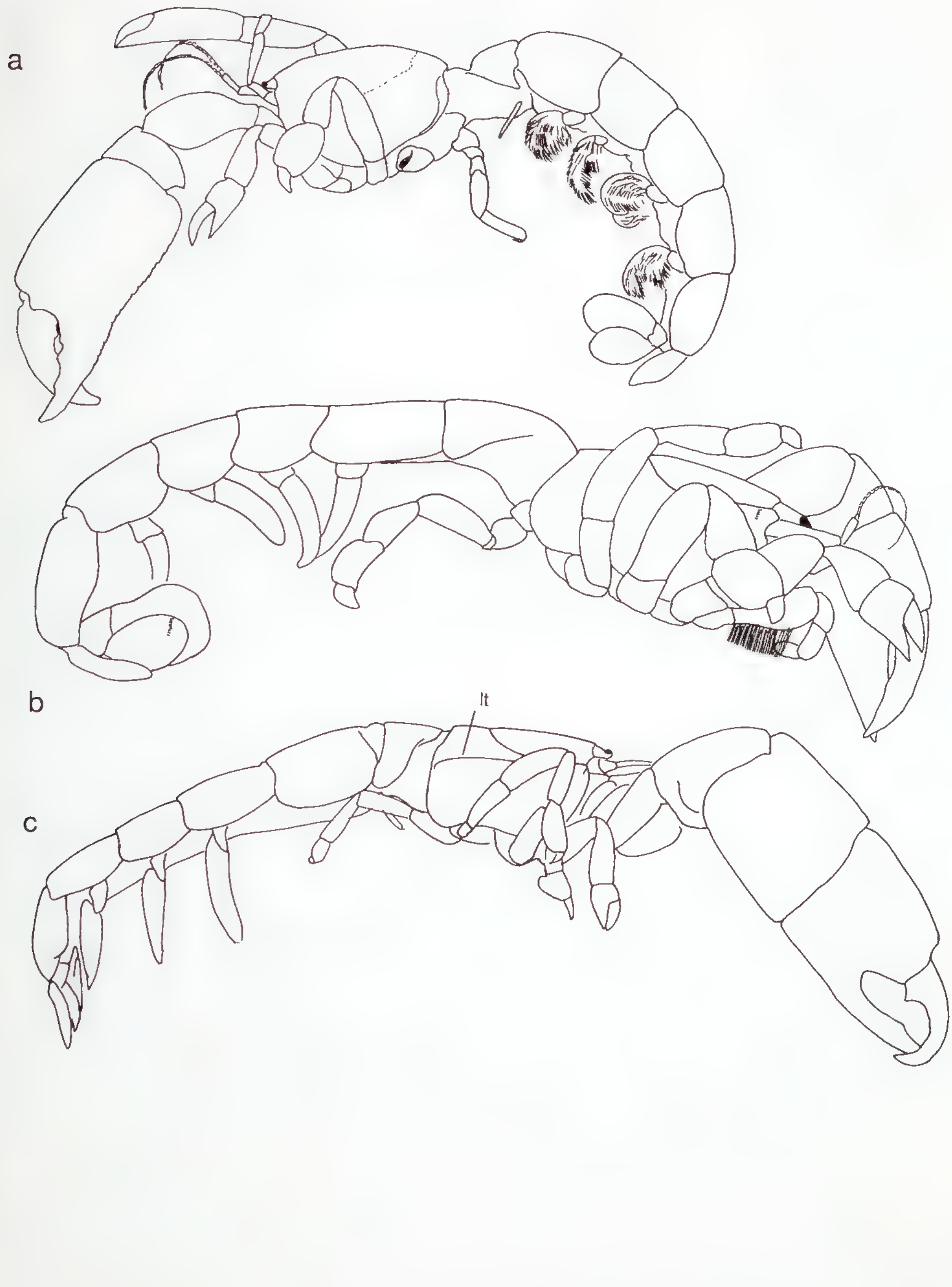
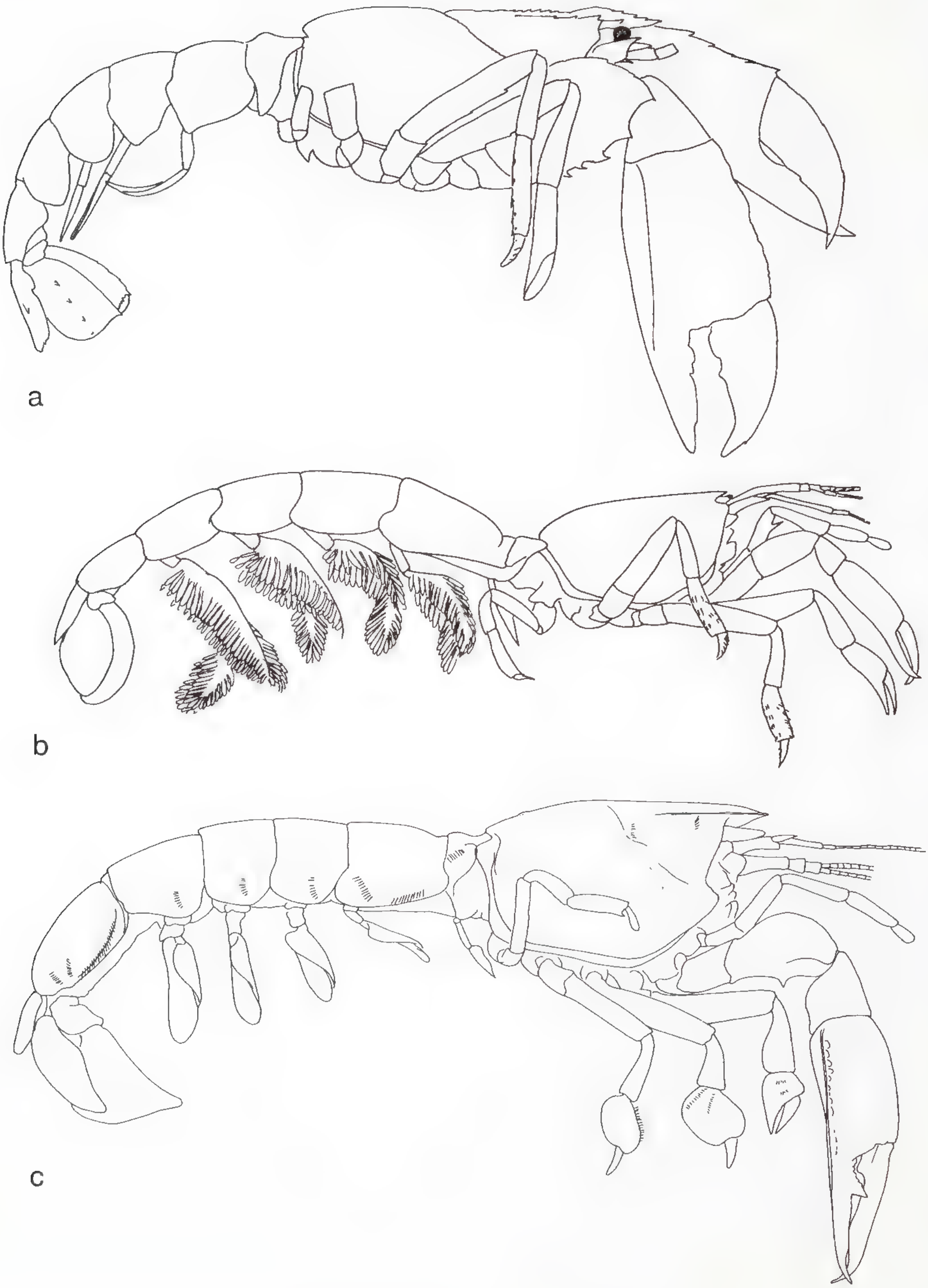


Figure 2. a, *Callianidea typa* Milne Edwards (Callianideidae) [after Sakai, 1992a]; b, *Thomassinia* sp. nov. (Thomassiniidae) c, *Trypaea australiensis* Dana (Callianassidae).
lt = linea thalassinica.



a

b

c

Figure 3. a, *Calaxius pailoeoensis* (Rathbun) (Axiidae) [after Sakai and de Saint Laurent, 1989]; b, *Michelea vanderoverae* (Gore) (Micheleidae); c, *Marcusiaxius lemoscastroi* Rodrigues and Carvalho (Micheleidae).

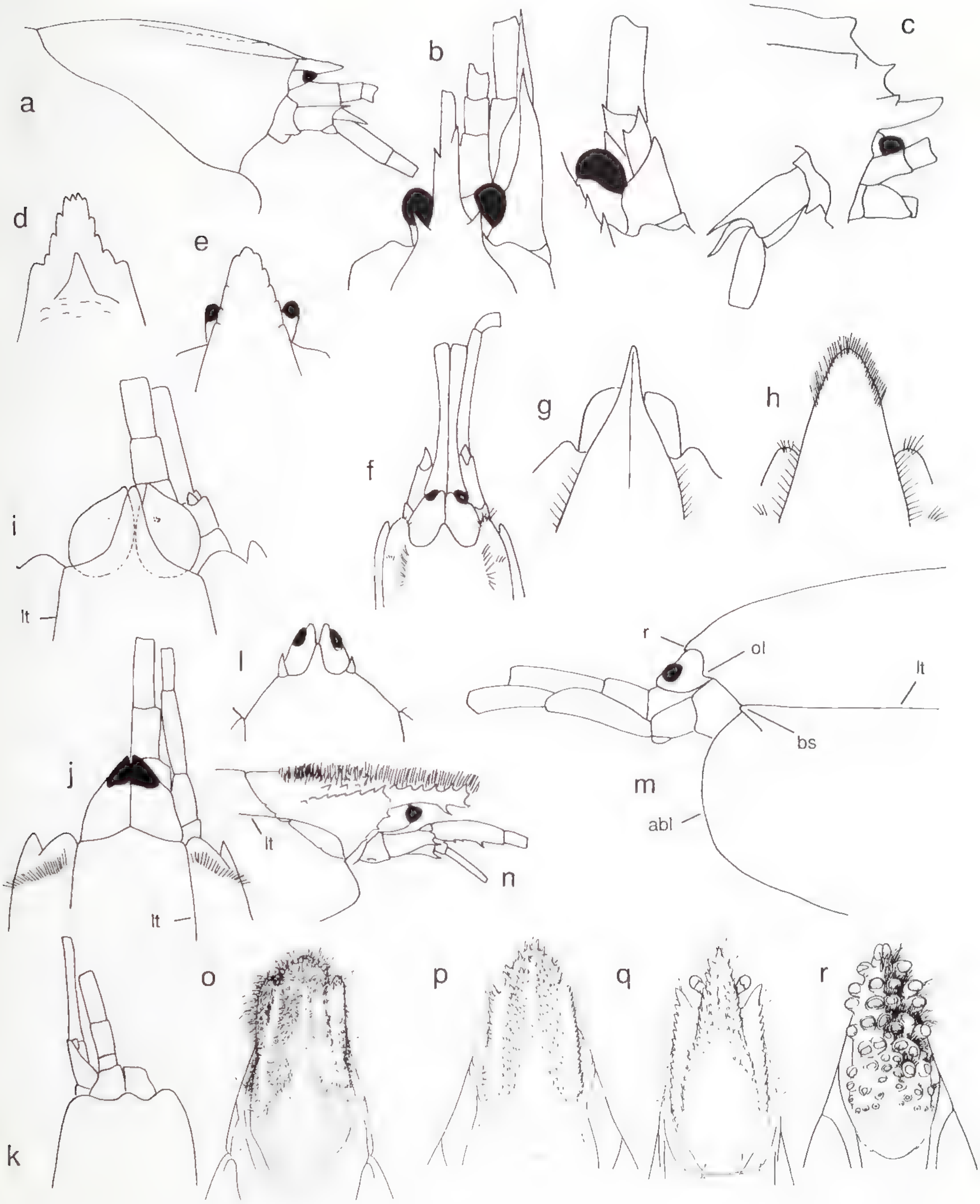


Figure 4. Anterior region of cephalothorax: a, *Axiopsis*; b, *Acanthaxius*; c, *Scytoleptus*; d, *Strahlaxius*; e, *Axius*; f, *Michelea*; g, *Meticonaxius*; h, *Marcusiaxius*; i, *Crosniera*; j, *Thomassinia*; k, *Callianidea*; l, *Corallianassa*; m, *Biffarius*; n, *Gebiacantha*; o, *Gebicula*; p, *Upogebia*; q, *Acutigebia*; r, *Tuerkayogebia* [o–r from Sakai, 1982].
Antenna 2 base and scaphocerite: s, *Eutrichocheles* (dorsal); t, *Spongiaxius* (lateral).
abl = anterior branchiostegal lobe; bs = branchiostegal scerite; lt = linea thalassinica; o = ocular lobe; r = rostrum.

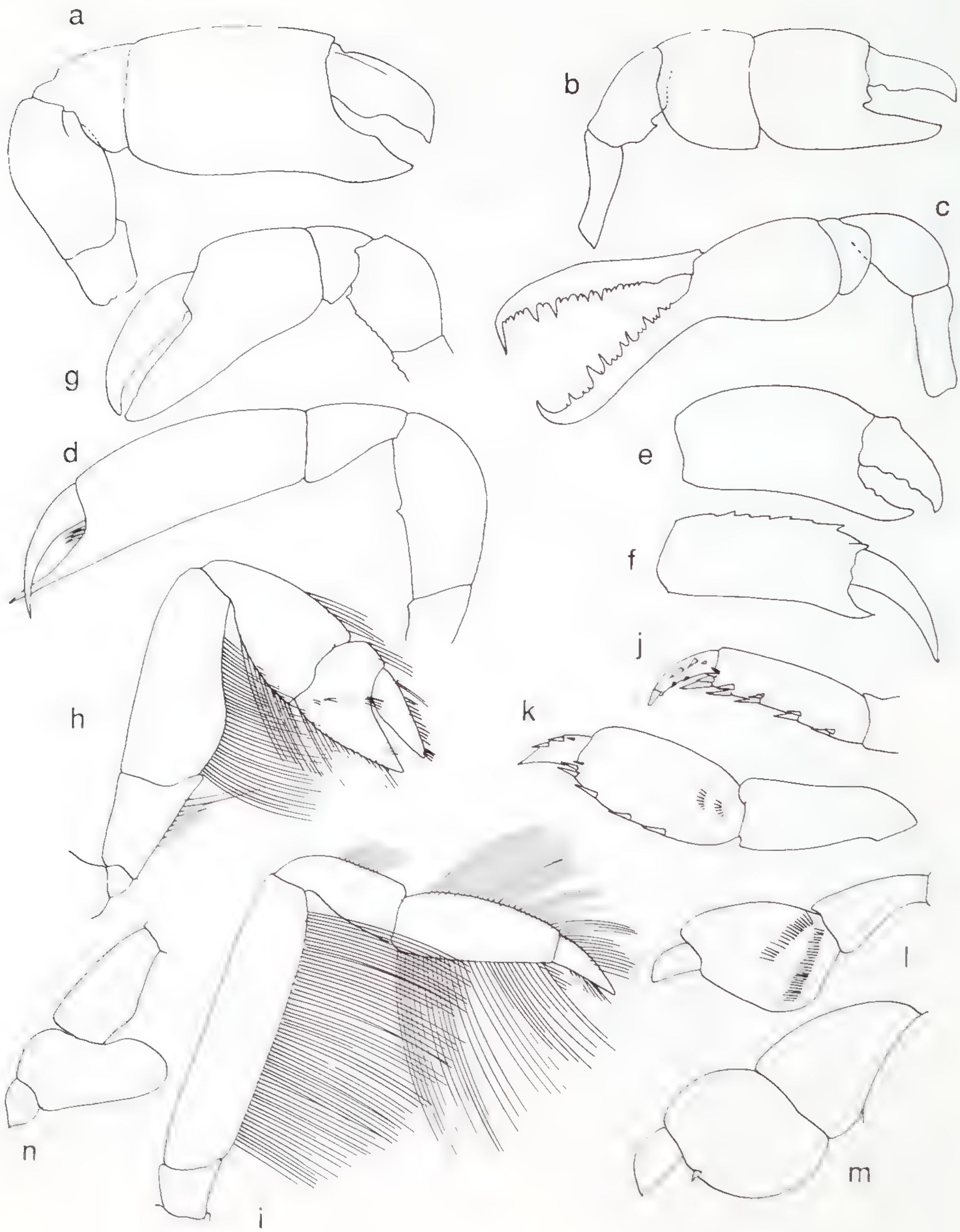


Figure 5. Major cheliped (pereopod 1): a, *Axius*; b, *Biffarius*; c, *Ctenocheles*; d, *Tethisea*; e, *Upogebia*; f, *Gebicula*.

Minor cheliped (pereopod 1): g, *Eiconaxius*.

Pereopod 2: h, *Callianassa*; i, *Upogebia*.

Pereopod 3 (distal articles showing spiniform setae and setal-rows): j, *Allaxius*; k, *Michelea*; l, *Marcusiaxius*; m, *Thomassinia*; n, *Callianassa*.

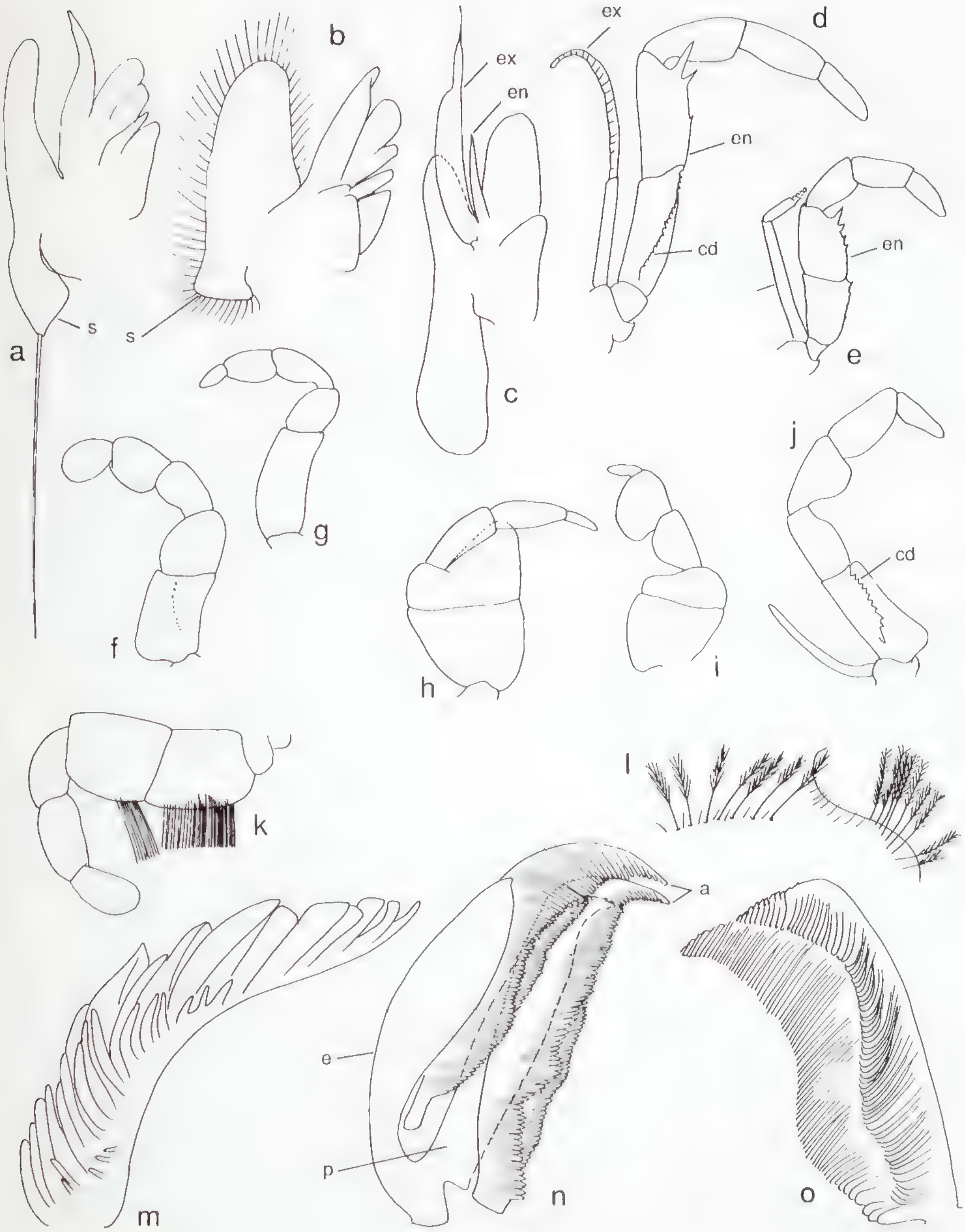


Figure 6. Maxilla 2: a, *Allaxius* (scaphocerite with long seta); b, *Callianassa* (scaphocerite with setose margin).
Maxilliped 1: c, *Allaxius* (with endopod and flagellate exopod).
Maxilliped 3: d, *Axiopsis*; e, *Coralaxius*; f, *Eucalliax*; g, *Anacalliax*; h *Trypaea*; i, *Callichirus*; j, *Gourretia*; k, *Thomassinia*.
Setal-rows at anterior margin of carapace: l, *Michelea*.
Branchiae on thoracomere 7: m, *Thalassina* (1 of 2 arthrobranchs); n, *Axius* (2 arthrobranchs and broad epipod with podobranch, dotted); o, *Biffarius* (1 of 2 arthrobranchs).
a = arthrobranch; cd = crista dentata; e = epipod; n = endopod; p = podobranch; s = scaphocerite; x = exopod.

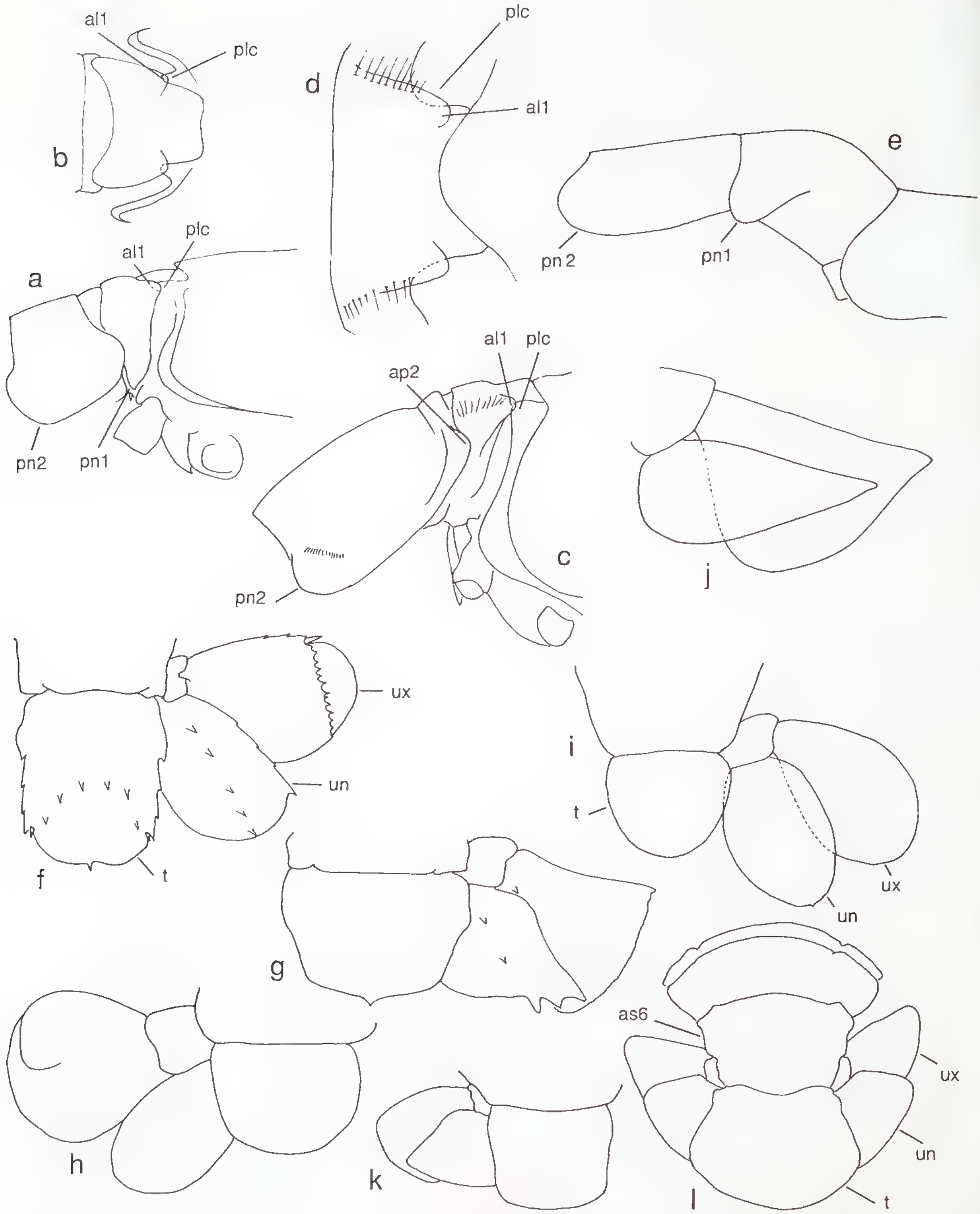


Figure 7. Posterior margin of carapace, abdominal somites 1 and 2: a, b, *Axius* (right and dorsal views); c, d, *Marcusiaxius* (right and dorsal views); e, *Thomassinia* (right view).

Telson and uropod: f, *Eutrichocheles*; g, *Strahlaxius*; h, *Biffarius*; i, *Michelea*; j, *Marcusiaxius* (right uropod only); k, *Upogebia*; l, *Pomatogebia*.

al1 = anterolateral lobe of abdominal somite 1; ap2 = anterior lobe of pleuron of abdominal somite 2; as6 = abdominal somite 6; dl = dorsal lobe; plc = posterolateral lobe of carapace; pn = pleuron; t = telson; un = uropodal endopod; ux = uropodal exopod.

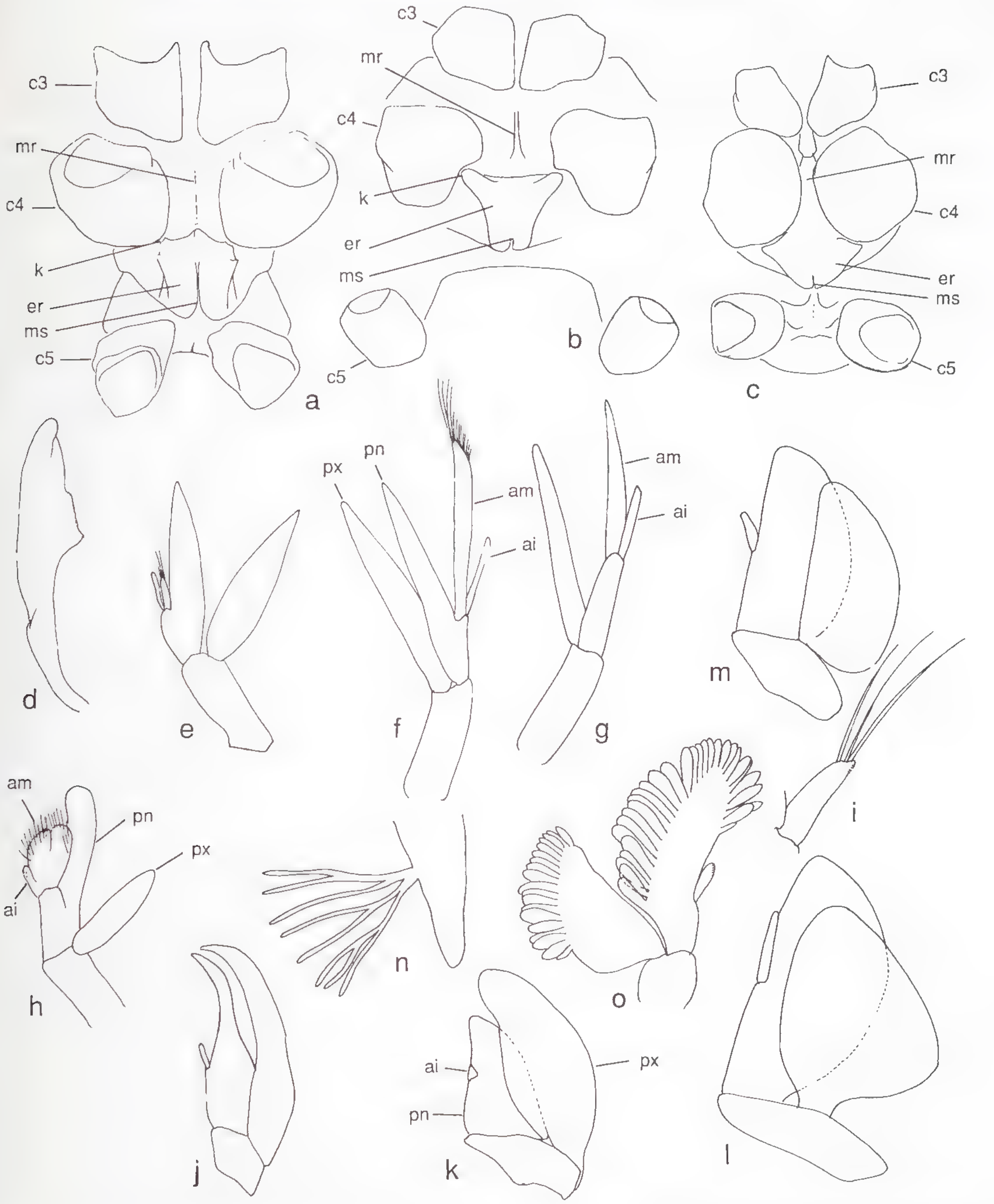


Figure 8. Sternites of thoracomeres 6, 7 and 8; coxae of pereopods 3 (top), 4 and 5 (bottom): a, *Axius*; b, *Biffarius*; c, *Callianidea*.

Pleopod 1 of male: d, *Bouvieraxius*.

Pleopod 2 of male, showing appendix interna and appendix masculina: e, *Axiopsis*; f, *Bouvieraxius*; g, *Calocaris*; h, *Coralaxius*; i, *Mictaxius* (combined appendices interna and masculina).

Pleopod 3, with appendix interna: j, *Biffarius*; k, *Anacalliax*; l, *Marcusiaxius*; m, *Neaxiopsis*.

Pleopodal marginal extensions: n, single branching filament on endopod of *Callianidea*; o, pleopod 2 of *Michelea* with marginal lamellae.

ai = appendix interna; am = appendix masculina; c3, c4, c5 = coxa of pereopods 3, 4, 5; er = episternal ridge (or plate); k = site of posterior condyle between sternite 7 and coxa 4; mr = median ridge of sternite 7; ms = median slit; pn, pleopodal endopod; px = pleopodal exopod.

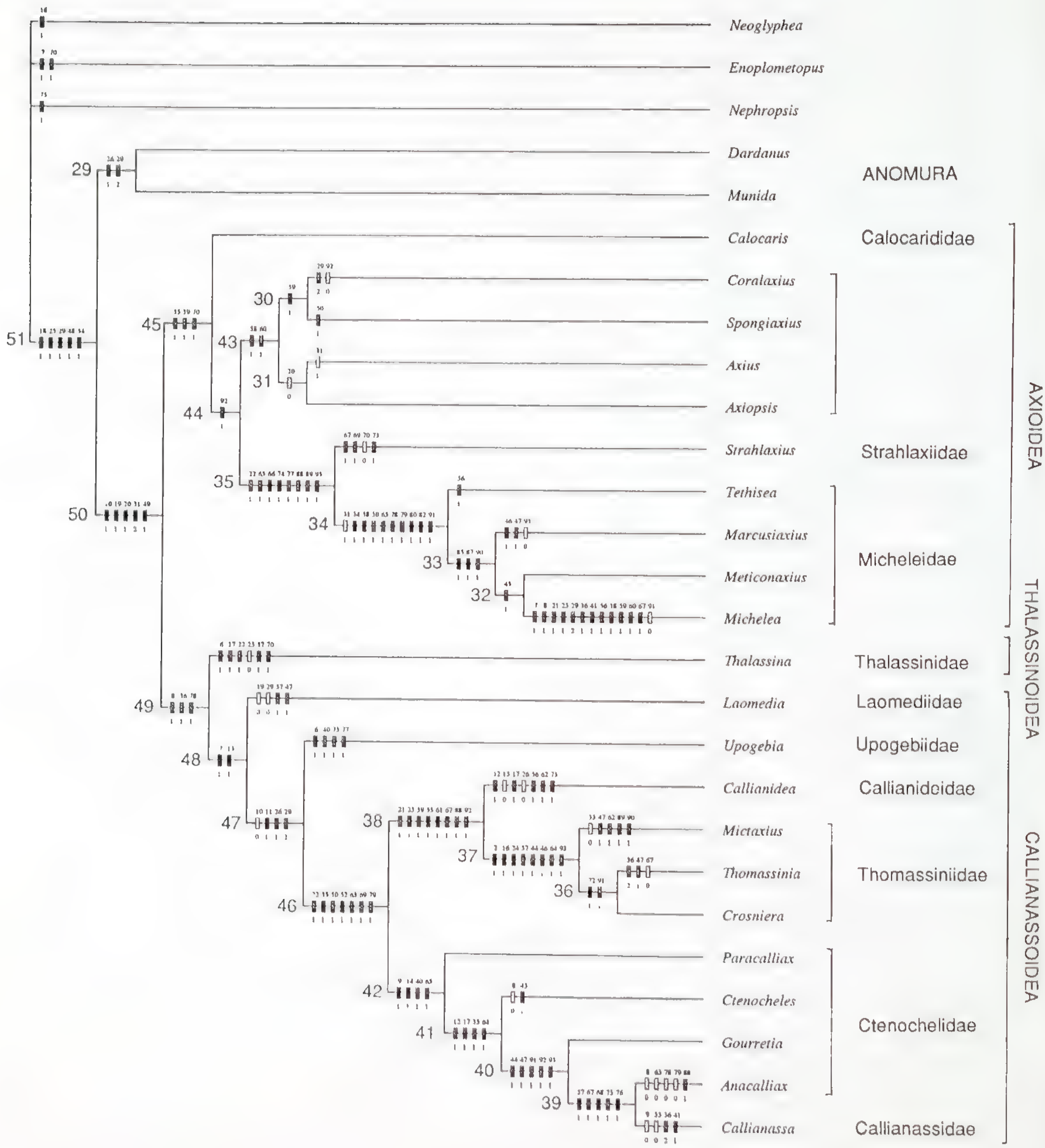


Figure 9. Cladogram of 22 selected genera of Thalassinidea and five outgroup genera generated from HENNIG86 using a single successive weighting of 97 characters. Unambivalent character changes are given for each ancestral clade. Clades are numbered at their stems and discussed in the text. Higher taxa are given at the right.

Memoirs of the Museum of Victoria 54:121–123 (1994)

XEINOSTOMA INOPINATUM SP. NOV., A NEW CRAB FROM RÉUNION ISLAND, SOUTH INDIAN OCEAN (CRUSTACEA: BRACHYURA: CYCLODORIPPIDAE: XEINOSTOMATINAE)

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Abstract

Tavares, M., 1994. *Xeinostoma inopinatum* sp. nov., a new crab from Réunion Island, south Indian Ocean (Crustacea: Brachyura: Cyclodorippidae: Xeinostomatinae). *Memoirs of the Museum of Victoria* 54: 121–123.

Xeinostoma inopinatum sp. nov., the second Indian Ocean species and fourth representative of the genus is described from four specimens collected during the Oceanographic Cruise *MD32/La Réunion 1982*, conducted off the coast of Réunion I., Indian Ocean, in depths between 165 and 750 m. The new species is compared with *X. eucheir* Stebbing, 1920, from South Africa and Madagascar, the type species of the genus.

Introduction

The Indo-West Pacific species of the family Cyclodorippidae Ortmann, 1892 were recently reviewed by Tavares (1991, 1992a, b, 1993). Twenty-three species are included in seven genera, all but *Corycodus* exclusively Indo-Pacific: *Tymolus* Stimpson, 1858; *Corycodus* A. Milne Edwards, 1880; *Genkaia* Miyake and Takeda, 1970; *Xeinostoma* Stebbing, 1920; *Krangalangia* Tavares, 1992; *Ketamia* Tavares, 1992 and *Phyllotymolinum* Tavares, 1993.

Until now, three species of *Xeinostoma* were known: *X. eucheir* Stebbing, 1920, from South Africa and Madagascar, *X. sakaii* Tavares, 1993 from Japan and the Philippines, and *X. richeri* Tavares, 1993 from Chesterfield and Loyalty Islands. The examination of additional material from the Indian Ocean collected during the Oceanographic Cruise *MD32/La Réunion 1982*, revealed the presence of an undescribed species from the Réunion Island, between 165 and 750 m deep. This new species is described here as *Xeinostoma inopinatum*.

The terms used in the description are those used by Tavares (1991). Measurements are of carapace length followed by carapace width (measured at the widest point, anterolateral tooth included) in millimetres. All the type material is deposited in the Muséum national d'Histoire naturelle, Paris (MNHN), except for one male paratype which is in the carcinological collection of the Universidade Santa Ursula, Rio de Janeiro (USU). Xeinostominae, incorrect original spelling, is corrected to Xeinostomatinae.

Xeinostoma inopinatum sp. nov.

Figure 1a–c

Material examined. Holotype. South Indian Ocean. MD32/La Réunion 1982 stn FA96: 19°41.5'S, 54°8.3'E, 350–750 m, 28 Aug 1982, MNHN-B 22662 (female, 4 x 4.5 mm).

Paratypes. MD32/La Réunion 1982 stn DS176: 21°1.7'S, 55°10.6'E, 165–195 m, 5 Sep 1982, MNHN-B 22663 (2 males, 2.5 x 2.7 mm, 3.8 x 4.0 mm); USU 406 (1 male, 2.4 x 2.6 mm).

Etymology. The specific name is Latin, unexpected.

Description. Carapace subcircular with dorsal face flat; widest point at level of anterolateral tooth. Limits between dorsal face and lateral walls of carapace weak. Front semicircular, bordered by small teeth. Fronto-orbital width greater than half maximal breadth of carapace. Frontal, gastric and cardiac regions covered with minute granules. Hepatic and branchial regions paved with rounded granules. Frontal region slightly depressed medially. Gastric pits inconspicuous. Gastric and cardiac regions outlined laterally by gentle furrow. Anterolateral tooth well developed and ornamented with small spines.

Exorbital tooth prominent and granulated. Orbits deeply excavated with superior and inferior margins well delimited; superior border wide, convex medially, notched at angle with frontal border. Eyestalk mobile, rather slender and bearing few granules. Antennule about half carapace length.

Prostomial chamber not reaching frontal

border of carapace. Exopod of second and first maxillipeds bearing large flagellum. Exopod of third maxilliped lacking flagellum.

Cheliped strong, armed with truncate tubercles and spines; internal margin of carpus with short triangular projection ending in 3 small spines. First and second walking legs similar, dactyli laterally compressed. Fourth and fifth pereopods very short and subdorsal, both with curved dactyli.

Female abdomen with 6 segments extremely narrow compared to carapace width. Sixth abdominal segment about twice as long as wide. In females, first pleopod vestigial and uniramous, inserted on ventral face of abdominal segment. Pleopods 2–5 biramous and articulated on lateral end of abdominal segments 2–5. Male abdomen of 5 segments.

Distribution. Known only from Réunion Island, south Indian Ocean, 165–750 m.

Remarks. Xeinostoma inopinatum sp. nov., is the second Indian Ocean species and the fourth representative of the genus. The following characters distinguish this new species from *X. eucheir*:

1, carapace with small and regularly distributed granules which are more strongly developed laterally (fig. 1a), while in *X. eucheir* the frontal (borders excepted), mesogastric and metagastric regions are smooth and the granules that cover the carapace are coarse (fig. 1d);

2, widest point of the carapace is at the level of

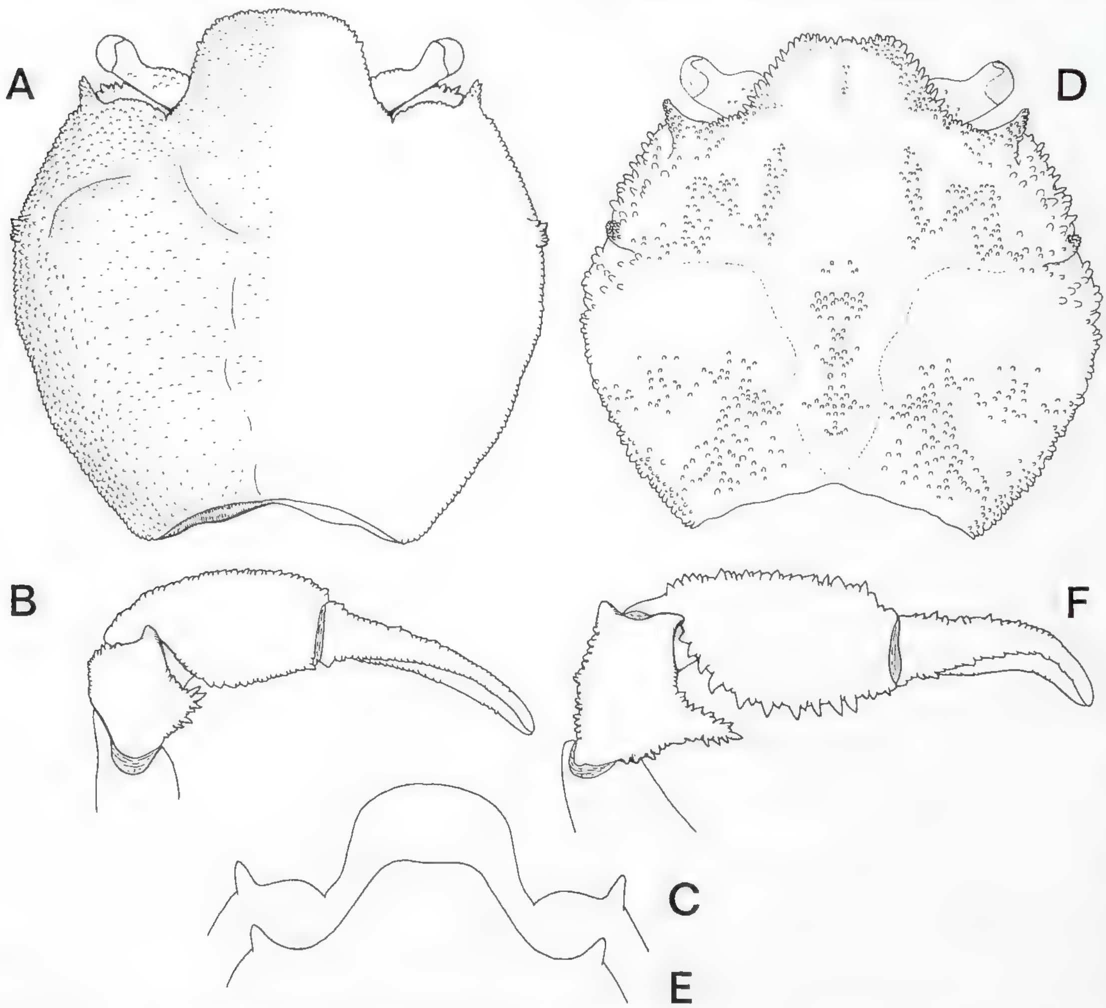

Figure 1. a—c. *Xeinostoma inopinatum* sp. nov., holotype (4 x 4.5mm). d, e. *Xeinostoma eucheir* Stebbing, 1920. South Africa, Cape Vidal, 144 m: male lectotype, 6.6 x 7.7 mm (BM 1928.12.1.195–196). f. *Xeinostoma eucheir* Stebbing, 1920. Madagascar, *Vauban*, 12°40'S, 48°18'E, 205–185 m: male 6.9 x 8.0 mm (MNHN-B 24596).

a, d, dorsal view of the carapace; b, f, outline of left cheliped; c, e, outline of fronto-orbital region of carapace.

the anterolateral tooth (fig. 1a), while in *X. eucheir* it is behind the anterolateral tooth (fig. 1d);

3, superior border of the orbit is wide, convex, and notched at the angle with the frontal border of the carapace (fig. 1c), while in *X. eucheir* the superior border of the orbit is narrow, concave and meets the frontal border of the carapace in a gentle curve (fig. 1e);

4, internal margin of the carpus of the cheliped with a short triangular projection ending in three small spines (fig. 1b), while in *X. eucheir* the margin of the carpus of the cheliped is armed with a very prominent triangular tooth that bears several acute spines (fig. 1f).

Among the seven Indo-Pacific genera of the Cyclodorippidae, two show a coincident distributional pattern in the south Indian Ocean: half or more of their species inhabit the same small area while their other representatives are known from a single locality outside of the Indian Ocean. Thus, three of the five species of *Corycodus* and two of the four species of *Xeinostoma* are found only in a relatively small area that includes a part of the eastern coast of South Africa near the Mozambique Channel, Madagascar and Réunion. The other species are found far away in the Caribbean and Sulu Seas (one species of *Corycodus* in each area) and Japan and New Caledonia (one species of *Xeinostoma* in each area).

Acknowledgements

I thank Michèle de Saint Laurent (Muséum national d'Histoire naturelle, Paris) who participated in the *MD32/La Réunion 1982* cruise, for calling my attention to this material; Alain Guille (Director of the Observatoire Océanologique de Banyuls, Banyuls-sur-Mer, France), cruise leader of *MD32/La Réunion 1982*, for making it available for study; and to Peter Castro (California State Polytechnic University, Pamona) for checking the English text.

I am grateful to Danièle Guinot (Paris) and Lipke B. Holthuis (Leiden) who commented on the manuscript with their usual interest. The manuscript also benefited from critical reading by two anonymous referees.

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Memoirs of the Museum of Victoria 54: 125–147 (1994)

ACANTHASPIDIIDAE (CRUSTACEA: ISOPODA) FROM THE CONTINENTAL SHELF AND SLOPE OF SOUTH-EASTERN AUSTRALIA WITH DESCRIPTION OF TWO NEW SPECIES

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Abstract

Brandt, A., 1994. Acanthaspidiidae (Crustacea: Isopoda) from the continental shelf and slope of south-eastern Australia with description of two new species. *Memoirs of the Museum of Victoria* 54: 125–147.

The presence of Acanthaspidiidae off the continental shelf of Australia is recorded. Two new species are described, *Ianthopsis franklinae* sp. nov., and *Ianthopsis kimblae* sp. nov. Material of a third new species whose range is reported is in too poor condition to allow complete description. In addition, acanthaspidiids from the Southern Ocean are reported from the Australian shelf: *Acanthaspidia drygalskii* Vanhöffen, 1914, and *Ianthopsis multispinosa* Vanhöffen, 1914.

Introduction

The family Acanthaspidiidae was established by Menzies (1962). Since many of the included species are incompletely described (e.g. Kussakin, 1982) and did not form a monophyletic unit, Brandt (1991) reviewed the family and synonymized three genera with *Acanthaspidia* Stebbing, 1898. This and *Ianthopsis* Beddard, 1886 are the only genera. Acanthaspidiid isopods occur predominantly in the deep sea but 19 species have been found on the continental shelf around Antarctica. Of these 17 species are endemic suggesting a probable radiation there (Brandt, 1992a). Three species have been reported from the Northern Hemisphere, two in the Atlantic. *A. typhlops* (Sars, 1879) is a comparatively derived species of the northern Atlantic and Pacific and most probably reached there via the deep Atlantic. The second is *I. pulchra* (Hansen, 1916). A study of recent samples from the Kolbeinsey Ridge, north of Iceland, and type material in the Zoological Museum of Copenhagen revealed that this species does not belong in Acanthaspidiidae (Brandt, 1993). The third, *A. hanseni* Birstein, 1963 is confined to the northern Pacific (Kussakin, 1988). The relationship between Antarctica and Australia and the probable origin of some taxa of Antarctic isopods was discussed in Brandt (1992a, b).

The material from south-eastern Australia is part of collections of about 350 species of isopods from slope depths of between 200 and 3150 metres and from shallower Bass Strait. Most collections were made using an epibenthic sled and the general environment was described by Poore et al. (in press). The collections are in the Museum of Victoria, Melbourne (NMV). It is supplemented by small collections from the Australian Museum, Sydney (AM).

Two species of Acanthaspidiidae previously known only from south of the Antarctic Convergence have been identified and descriptions of two new species are presented here. Another species occurs in the samples but unfortunately its condition is too poor to describe.

Acanthaspidia Stebbing, 1898

Acanthaspidia drygalskii Vanhöffen

Acanthaspidia drygalskii Vanhöffen, 1914: 68–69. — Menzies, 1962: 177. — Wolff, 1962: 258. — Kussakin, 1967: 340 [342]. — Brandt, 1991: 210–217, figs 1–5.

Exacanthaspidia rostratus Menzies and Schultz, 1968: 171–174, figs 25, 26.

Material examined. Victoria. 96 km S of Point Hicks (38°40.29'S, 149°18.06'E), 2900 m, compacted clay, WHOI epibenthic sled, G. C. B. Poore et al. on ORV *Franklin*, 25 Oct 1988 (stn SLOPE 66), NMV J20170 (1); 76 km S of Point Hicks (38°29.33'S, 149°19.98'E), 1840 m, sandy mud, fine shell, WHOI epibenthic sled, G. C. B. Poore et al. on ORV *Franklin*, 26 Oct 1988 (stn SLOPE 69), NMV J20171, (1).

Distribution. Gauss Station, Bellingshausen Sea (66°S, 89°W), Weddell Sea, Antarctic Indian Ocean; Australia, slope east of Bass Strait, 1840–2900 metres depth.

Remarks. These records extend the distribution outside the Southern Ocean where it was hitherto known only in the Pacific and Indian Ocean sectors. The presence of *A. drygalskii* in deep southern Australian waters is probably the result

of a vicariance event. This means that *Acanthaspidia* has existed since the Tertiary, before Australia and Antarctica separated about 55 million years ago and the circumpolar current became effective in the East Antarctic (Brandt, 1992b; Crame, 1989, 1992).

This species can be distinguised by the strongly serrated head, pereonites, and a pleotelson which is broader than in other species of *Acanthaspidia* (for further characters see Brandt, 1991, 1992a).

Ianthopsis Beddard, 1886

Ianthopsis franklinae sp. nov.

Figures 1–8

Material examined. Holotype. Victoria. 67 km S of Point Hicks (38°23.95'S, 149°17.02'E), 1277 m, fine mud, WHOI epibenthic sled, 25 Oct 1988 (stn SLOPE 67), NMV J13269 (female, 6.00 mm).

Paratypes. Same details as holotype, NMV J13270 (allotype male); NMV J20181 (2).

New South Wales. Off Nowra (35°0.0'S, 151°16.3'E), 1100 m, 5 m otter trawl, 15 Jul 1986 (stn SLOPE 9), NMV J20175 (1). Off Eden (36°57,1'S, 150°23.4'E), 2000 m, epibenthic sled, W. Ponder et al. on ORV *Franklin*, 12 Dec 1986 (stn FR1086-09), AM P42268 (1 juvenile, 2.5 mm). E of Broken Bay (33°43'S, 151°46'E), 174 m, trawl, 19 Dec 1985, FRV *Kapala* (stn AM K85-21-05), AM P38893 (male), AM P42276 (1).

Victoria. 67 km S of Point Hicks (38°21.9'S, 149°20.0'E), 1000 m, 23 Jul 1986 (stn SLOPE 32), NMV J20177 (3); (38°31.6'S, 149°23.8'E), 1960 m, 8 m rectangular midwater trawl (on bottom), 21 Jul 1986 (stn SLOPE 23), NMV J20176 (2); (38°19.6'S, 149°24.3'E), 930 m, rock, rubble, clay, sand, biogenic sed., 23 Jul 1986 (stn SLOPE 33), NMV J20178 (3); (38°16.4'S, 149°27.6'E), 800 m, coarse shell, biogenic sediment, 23 Jul 1986 (stn SLOPE 34), NMV J20179 (1).

Tasmania. Off Freycinet Peninsula (42°2.2'S, 148°38.7'E), 800 m, coarse shelly sand, 27 Jul 1986 (stn SLOPE 45), NMV J20180, (2); 48 km ENE of Cape Tourville (42°00.25'S, 148°43.55'E), 1264 m, gravel with lumps of sandy mud aggregate, 30 Oct 1988 (stn SLOPE 81), NMV J20182 (8); 48 km ENE of Cape Tourville (42°00.25'S, 148°43.55'E), 1264 m, gravel with lumps of sandy mud aggregate, 30 Oct 1988 (stn SLOPE 81), NMV J23841 (female).

[All material collected using WHOI epibenthic sled by G. C. B. Poore, M. F. Gomon et al. on ORV *Franklin* unless otherwise noted.]

Description. Adult body length (measured from rostrum to tip of pleotelson) 6–8 mm (juveniles 2.5–3.5 mm); length 2.5 (female) – 2.6 (precopulatory male) times width (Figs 1; 6) (measurements after Hessler (1979), and Wilson and Hessler (1980)). Body depth about 0.2 times length. Pleotelson width 0.6 (female and male) times body width; as wide as long. Body with very short setules on margins and on long acute spines. Head with slightly serrate, acute anterodorsally bent spine; pereonite 1 with 2 mediolateral spines and 2 spine-like elevations on both sides (not developed in precopulatory male). Pereonites 2–4 with 3 spines (frontomedial and 2 mediolateral). Pereonites 5–7 with 1 medial spine. All pereonites with 2 acute lateral spines. Pereonite 1 medially slightly longer than pereonites 2–7, not fused with head; pleotelson smooth.

Antenna 1 (Figs 1; 6) 0.2 body length, of 8 articles (female), 9 articles (male); with more aesthetases in male than in female; article 1 shorter than 2, 1 broom seta and some simple setae in female (male without setation); article 2 1.1 (female) – 1.3 (male) times as long as article 1, with 1 lateral and 3 distal broom and some simple setae; article 3 almost twice as long as 4, with lateral simple seta (male), none in female; article 4 with lateral broom setae; article 5 about 4 times as long as 4, in male slightly longer than in female, female without, male with 1 aesthetasc; article 6 in female only slightly shorter than 5, in male three-quarters as long as 5; following articles decreasing in length and width, with 1 aesthetasc and 2 simple setae each; last article with 1 aesthetasc, simple setae and 1 short broom seta in both sexes.

Antenna 2 (Fig. 1) conjoint (compare Brandt, 1991), of 23 articles in female, (broken in paratype male), with short articles 1 and 2, without setae; article 3 almost twice as long as 2, antennal scale rudimentary, only lateral short blunt spine bearing another 2 long distal setae; article 4 about as long as 2, with some setae; article 5 as long as 6, both with simple setae on medial and lateral margins, article 6 with 2 distodorsal broom setae, 1 medially and 1 laterally; first flagellar article conjoint (new flagellar articles are build here during growth), with lateral and medial groups of simple long setae; group of 5 setae medially on almost every flagellar article; last article with some simple setae.

Left mandible (Figs 2; 6) with 4 cusps on incisor process in female, (3 in male); right mandible with 5 in both sexes; lacinia mobilis shorter than incisor in male, in female as long as incisor, with 4 cusps in male and 3 in female; left spine row of male with 8 members in left and 9 members in right mandible (Figs 2; 6), female with 7 on left and 9 on right mandible; molar processes slightly acuminating, medially concave, posterior margin of molar with 4 (left) and 5 (right mandible) setae in both sexes, lateral cutting surfaces of molar process with blunt spines

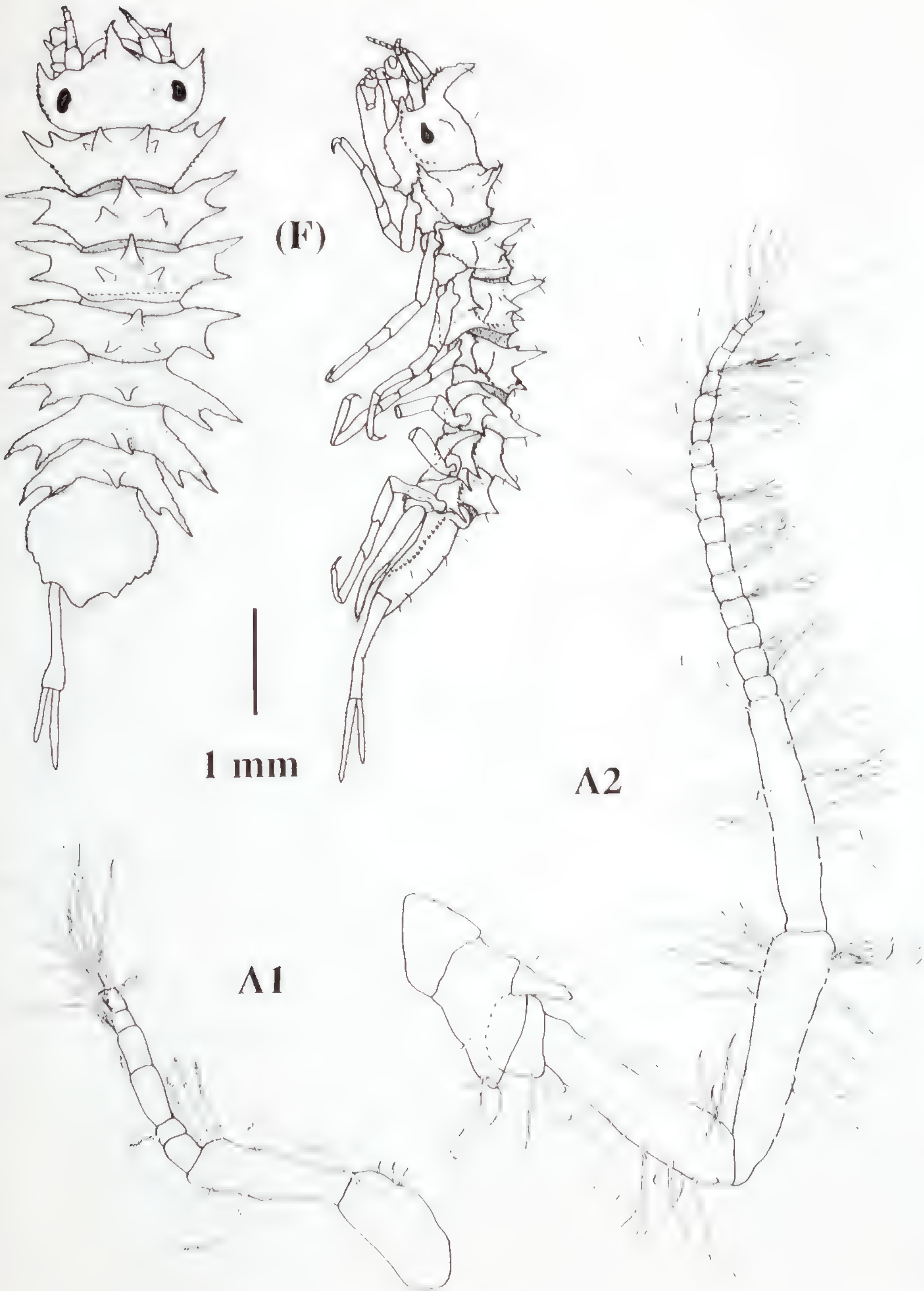

Figure 1. *Ianthopsis franklinae* sp. nov., holotype female in dorsal and lateral view, antenna 1 and antenna 2 of paratype female; NMV J13269.

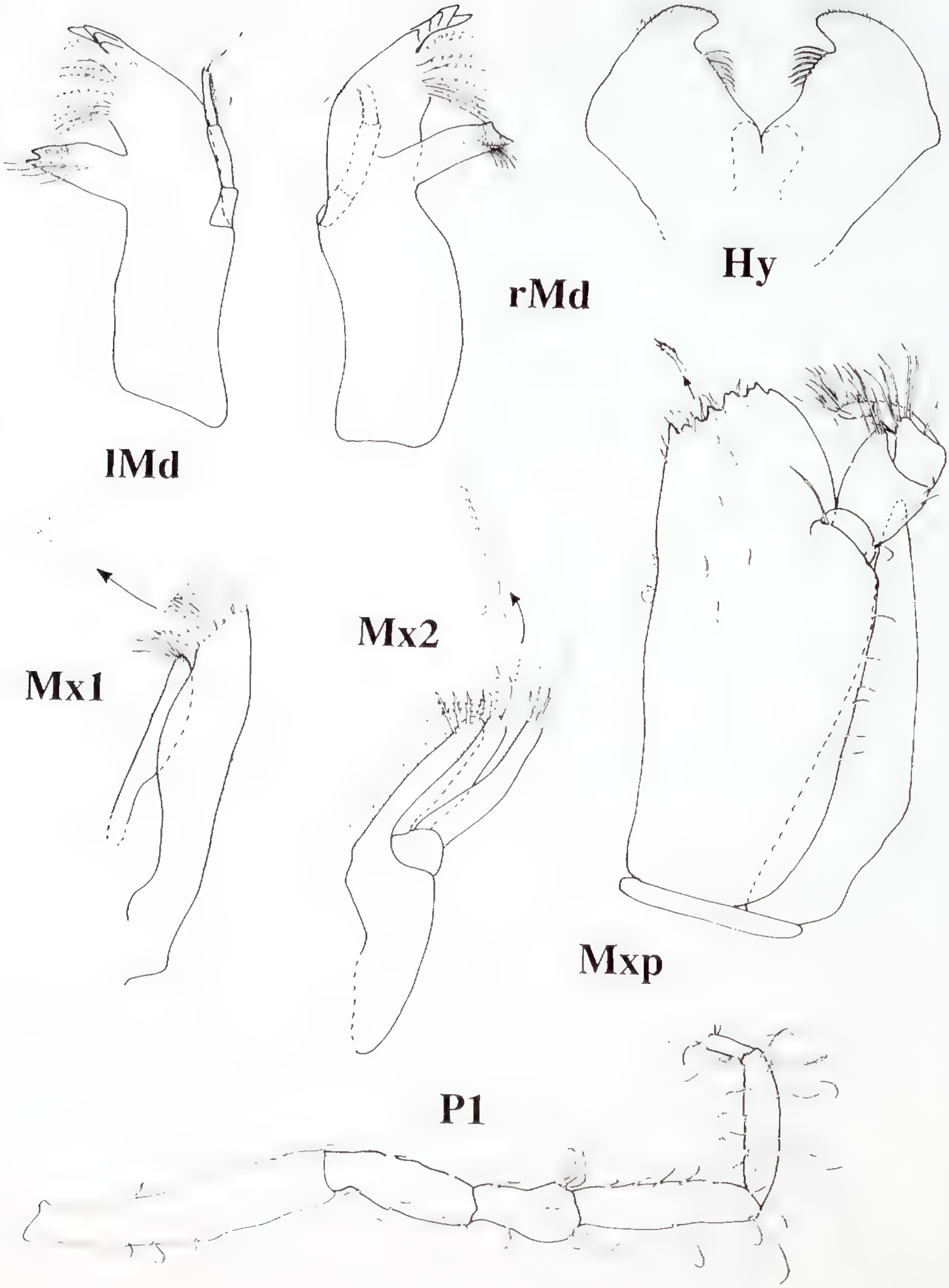

Figure 2. *Ianthopsis franklinae* sp. nov., paratype female, both mandibles, hypopharynx, maxilla 1, maxilla 2, maxilliped, and pereopod 1; NMV J13270.

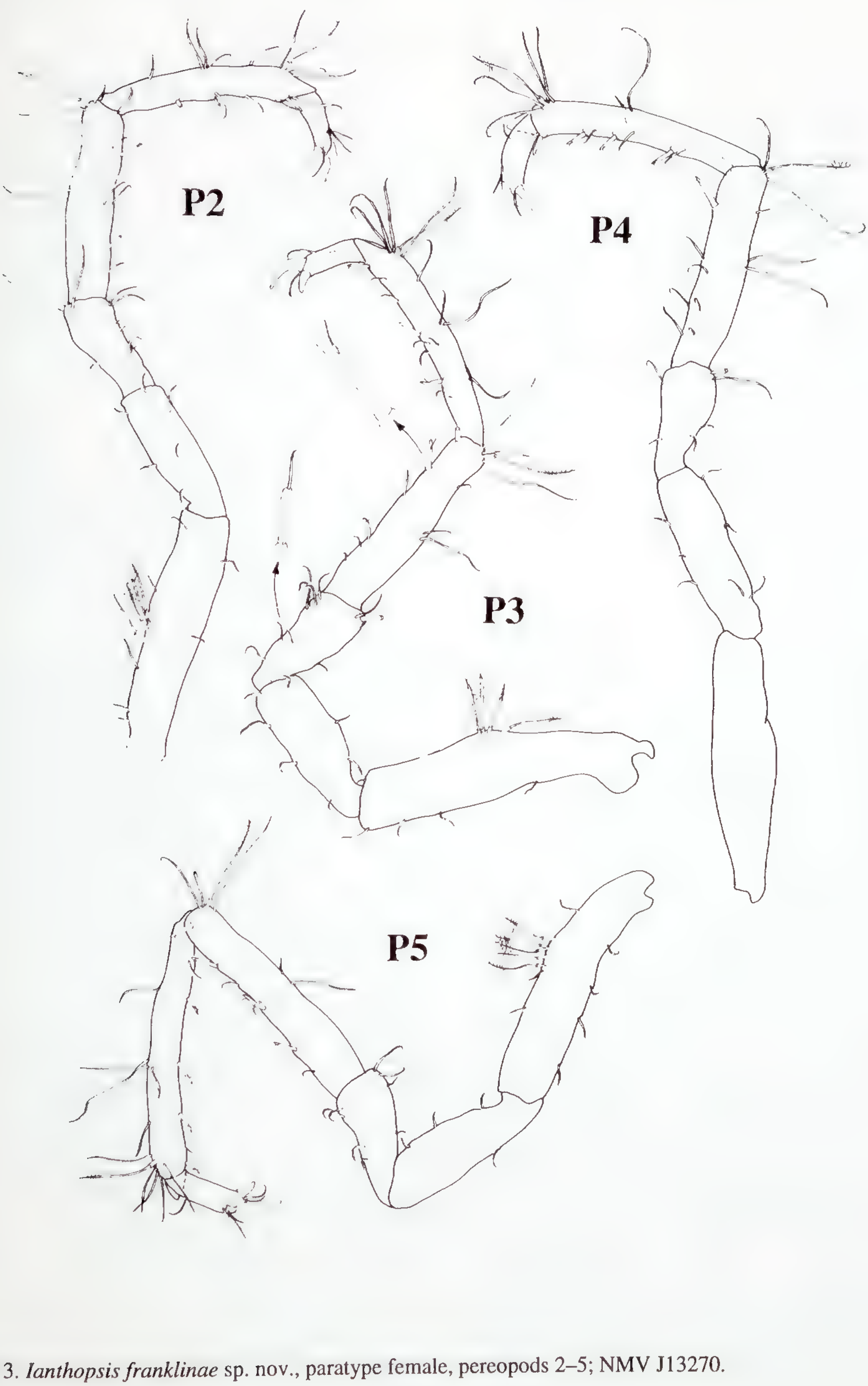

Figure 3. *Ianthopsis franklinae* sp. nov., paratype female, pereopods 2–5; NMV J13270.

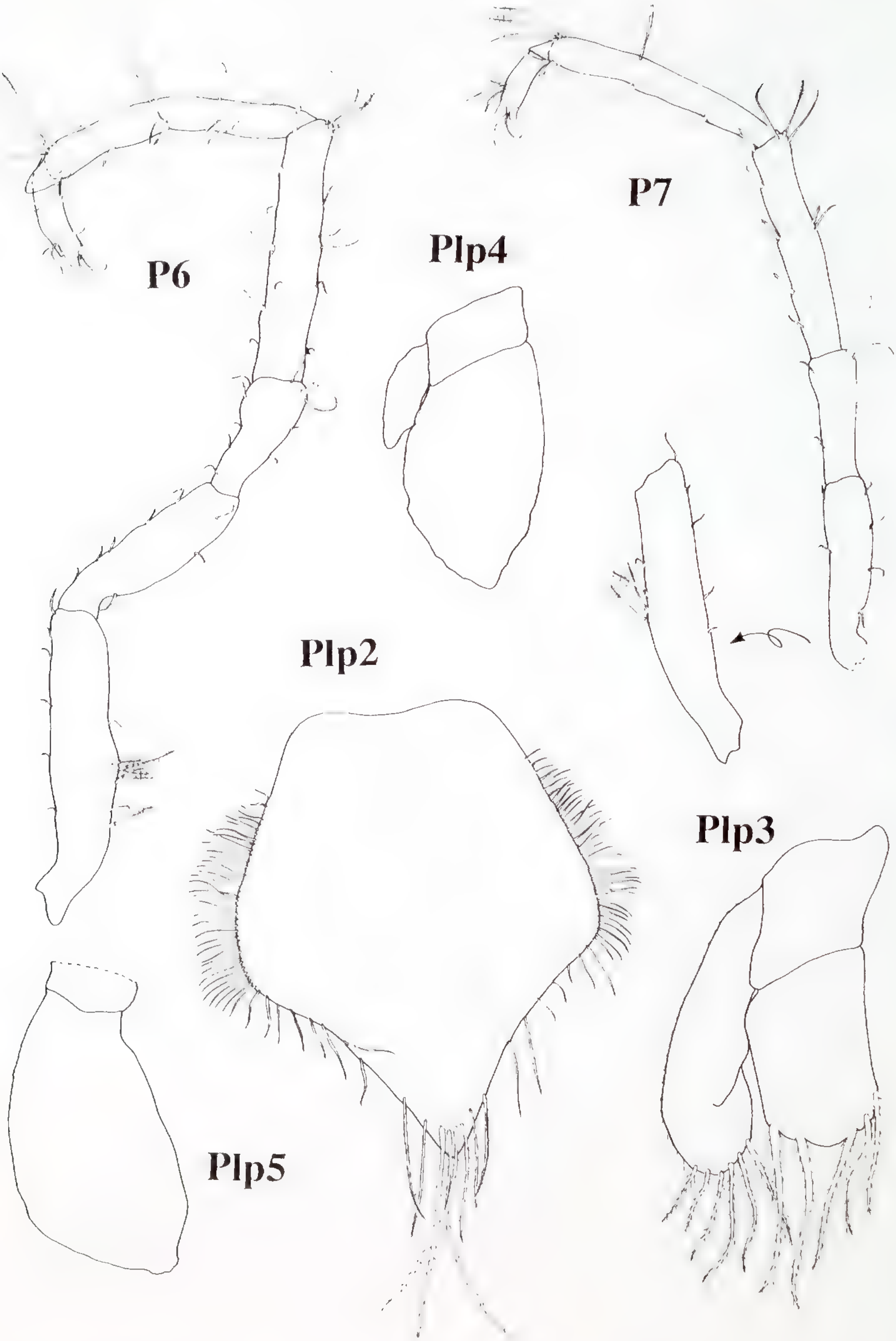

Figure 4. *Ianthopsis franklinae* sp. nov., paratype female, pereopods 6 and 7, pleopods 2–5; NMV J13270.

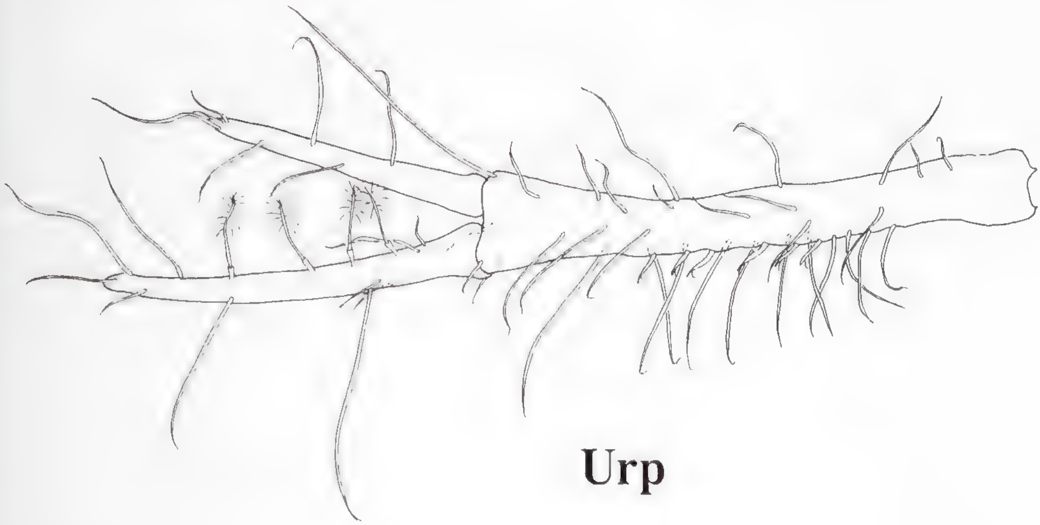

Figure 5. *Ianthopsis franklinae* sp. nov., paratype female, uropod; NMV J13270.

and notches; condyle length 0.1 mandibular body length, length of palp 0.4 mandibular body length. Palp article 1 without setation; article 2 longer than article 1, with 1 simple seta; palp article 3 slightly longer than 1.

Hypopharynx (Figs 2; 6) of 2 inner and 2 outer lobes, outer lobe medially concave and covered by many short simple setae.

Maxilla 1 (Figs 2; 6) inner endite half as wide as outer endite in both sexes; outer endite of male and female with 12 strong spine-like setae, some spinulose; inner endite with 4 strong setae in female (3 in male) and many slender long simple ones.

Maxilla 2 (Figs 2; 6) inner endite only slightly shorter and broader than medial and outer endites, with 4 distal strong spinulose spine-like setae in female, medial and outer endites with 4 strong spine-like, medially serrated setae of varying lengths.

Maxilliped (Figs 2; 6) basis twice as long as wide in both sexes, with few setae in distomedial half of basis, 3 coupling hooks, and 8 (female), or 6 (male) short fan-like setae distally. Palp article 1 as long as last; palp article 2 broadest, slightly shorter than 3; article 3 and 4 about subequal in length; article 5 narrowest, half as long as 4. Epipod slender and acuminating, length 4.1 times width and 0.7 times total basis length.

Pereopod 1 (Figs 2–4; 7) basis 0.17 (male) and 0.14 (female) times body length; pereopods 2–7 bases length to body length ratio in female about 0.2 respectively. Pereopod 1 (Figs 2; 7) length 0.6 times body length in both sexes; carpus: basis ratio about 0.6 in female and 0.9 in male; dactylus: propodus ratio 0.5 in both sexes. Dactylus bearing 2 distal claws with 2 sensillae between, anterior claw about twice as long as posterior one. Pereopod 2 (Figs 3; 7) length 0.7 body length in both sexes. Carpus: basis ratio 0.8 in both sexes; dactylus 0.3 propodus length in both sexes, as in preceding pereopod. Pereopod 3 (Figs 3; 7) length 0.8 body length; carpus: basis ratio 0.8; dactylus length 0.4 propodus length, otherwise as in preceding pereopods. Pereopod 4 (Figs 3; 7) length 0.8 body length; carpus: basis ratio 0.8; dactylus as in preceding pereopod. Pereopod 5 (Figs 3; 8) length 0.8 body length; carpus: basis ratio 0.9; dactylus as in preceding pereopod. Pereopod 6 (Figs 4; 7) of female (male broken) length 0.9 body length; carpus: basis 0.8; dactylus as in preceding pereopod. Pereopod 7 (Figs 4; 7) of female (male broken) length 0.8 body length; carpus: basis ratio 0.8; dactylus as in preceding pereopod.

Male pleopod 1 (Fig. 8) (precopulatory male) narrowing over distal third; length 2.3 proximal width, distal width 0.3 proximal width; apex

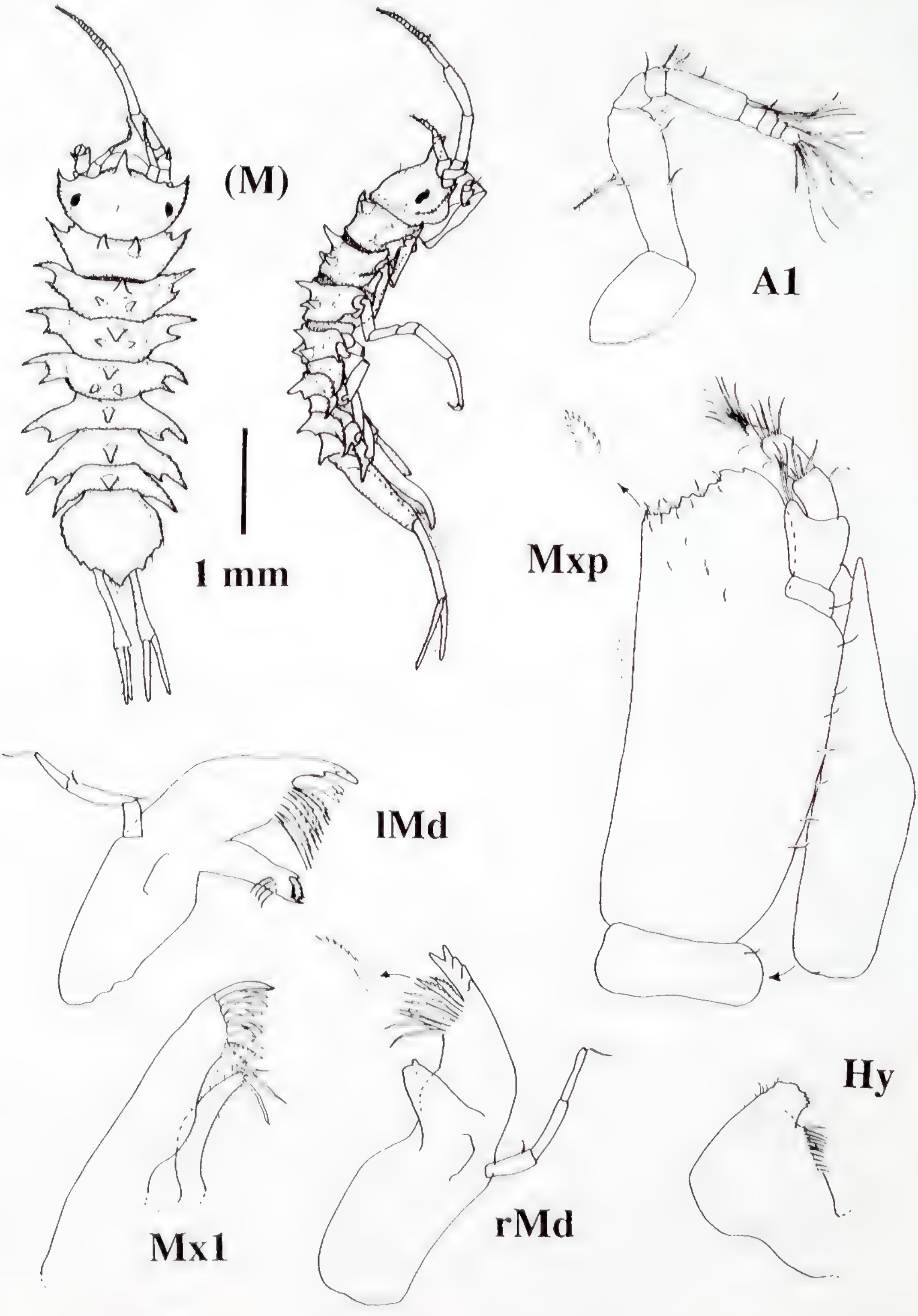

Figure 6. *Ianthopsis franklinae* sp. nov., paratype male in dorsal and lateral view, antenna 1, both mandibles, hypopharynx, maxilla 1, maxilliped; AM P38893.

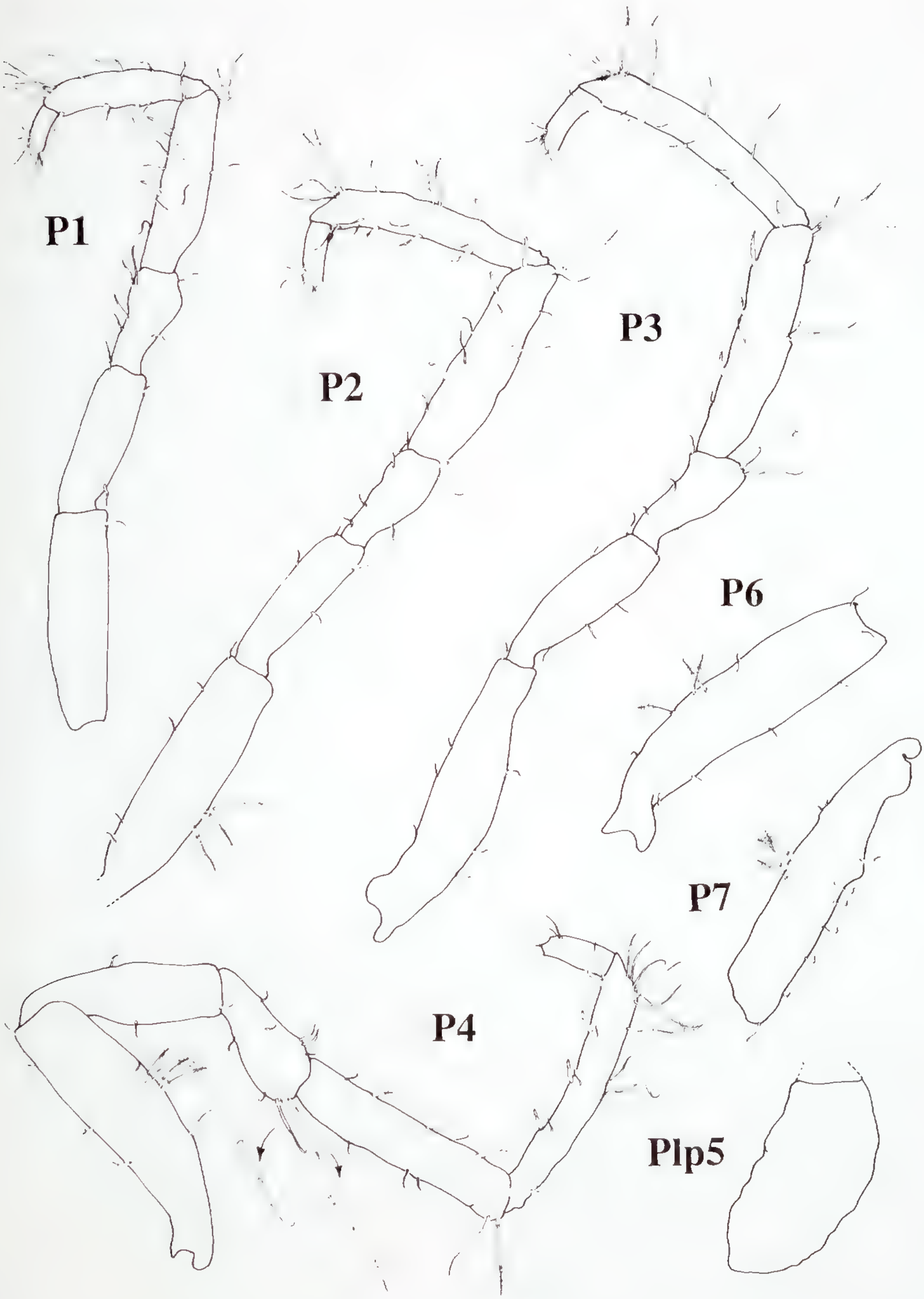

Figure 7. *Ianthopsis franklinae* sp. nov., paratype male, pereopods 1–4, bases of pereopods 6 and 7, pleopod 5; AM P38893.

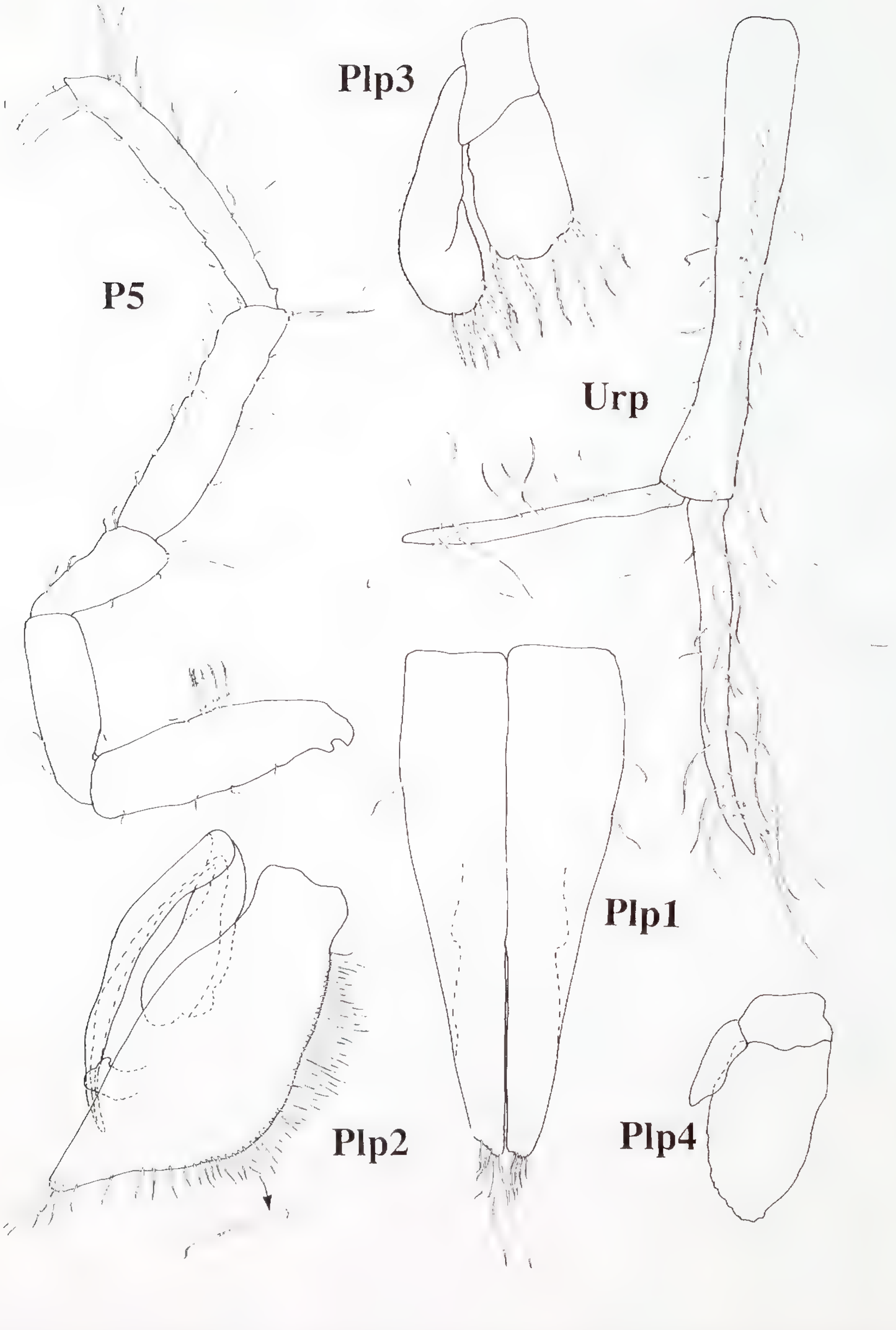

Figure 8. *Ianthopsis franklinae* sp. nov., paratype male, pereopod 5, pleopods 1–4, uropod; AM P38893.

almost straight; apical row of long simple setae, some proximolateral simple setae.

Male pleopod 2 (Fig. 8) (precopulatory male) peduncle length 2.5 width; lateral margin slightly rounded with many whip setae. Endopod inserting half length of peduncle; stylet not yet fully developed, shorter than peduncle. Exopod small, bilobed, without tuft of fine setae.

Female pleopod 2 (Fig. 4) anterior surface without setae, with slight medial furrow, lateral margins of pleopod with simple, distal tip with 8 long plumose setae, bearing only few setules; 1.2 times as long as wide.

Pleopod 3 (Figs 4; 8) of both sexes distomedial margin of exopod surrounded with fine setules. Endopod with 6 distal plumose setae in male and 5 in female, exopod more slender than endopod, distally with 6 plumose setae. Pleopod 4 (Figs 4; 8) of both sexes with short, rectangular peduncle. Exopod narrower and less than half as long as endopod, both rami without setae. Pleopod 5 (Figs 4; 7) of both sexes an oval lobe without setae.

Uropod (Figs 5; 8) 10 times as long as wide. Peduncle surrounded by many long simple setae, most laterally, female also with lateral row of sensory setae. Endopod 0.8 peduncle length, with proximolateral row of 4 broom setae in female (male without), exopod 0.8 times as long as endopod, long simple setae on both rami.

Distribution. South-eastern Australia (35°–42°S), 800–1277 metres depth.

Etymology. For ORV *Franklin*, the oceanographic vessel from which these samples were taken.

Remarks. Ianthopsis franklinae has a pattern of spines similar to that of *Ianthopsis multispinosa* Vanhöffen, 1914 but differs in the possession of small eyes (lacking in *I. multispinosa*). Moreover, the spines are smaller and more slender in the new species. The lateral epimera are longer and more pronounced and the lateral pleotelsonic margins are more deeply serrated in *I. multispinosa* than in the new species. All other known species of *Ianthopsis* bear no, very small, or fewer spines than the new species.

Ianthopsis kimblae sp. nov.

Figures 9–17

Material examined. Holotype. New South Wales. 44 km E of Nowra (34°55.79'S, 151°08.06'E), 429 m, muddy coarse shell, WHOI epibenthic sled, 22 Oct 1988 (stn SLOPE 56), NMV J13271 (male, 3.0 mm).

Paratypes. Same details as holotype, NMV J13272 (female allotype, 2.9 mm), NMV J20188 (129 females, 2.5–3 mm; 45 males, 1.8–2.8 mm; 5 mancas, 1.0–1.2 mm), NMV J36436 (female), NMV J36437 (male), NMV J36438 (female ovig.).

Other material. New South Wales. Off Eden (37°07.3'S, 150°20.2'E), 520 m, grey coarse shell, 20 Jul 1986 (stn SLOPE 19), NMV J20184 (4); (37°0.6'S, 150°20.7'E), 363 m, coarse shell, 21 Jul 1986 (stn SLOPE 22), NMV J20191 (10); Off Nowra (34°57.9'S, 151°8.0'E), 503 m, bryozoa and shell, 14 Jul 1986 (stn SLOPE 2), NMV J20183 (8).

Victoria. S of Point Hicks (38°14.8'S, 149°9.3'E), 200 m, coarse sand, gravel, 24 Jul 1986 (stn SLOPE 41), NMV J20186 (3); (38°17.70'S, 149°11.30'E), 400 m, coarse sand, gravel, mud, many sponges, 24 Jul 1986 (stn SLOPE 40), NMV J20185 (138); NMV J23842 (male A).

Tasmania. Eastern Bass Strait, 60 km E of North Point, Flinders I. (39°41.7'S, 148°39.5'E), 115 m, muddy sand, naturalist's dredge, G. C. B. Poore on HMAS *Kimbla*, 27 Mar 1979 (stn BSS 32), NMV J20189 (2); 63 km E of North Point, Flinders I. (39°44.8'S, 148°40.6'E), 124 m, R. Wilson on RV *Tangaroa*, 14 Nov 1981 (stn BSS 167), NMV J20190, (19); 50 km NE of Babel I. (39°40.3'S, 148°46.5'E), 293 m, rock, coarse sand, naturalists' dredge, G. C. B. Poore on HMAS *Kimbla*, 27 Mar 1979 (stn BSS 33), NMV J20192 (2).

[All material collected using WHOI epibenthic sled by G. C. B. Poore, M. F. Gomon et al. on RV *Franklin* unless otherwise noted.]

Description. Adult body (Figs 9; 14; figure 17 shows the dorsal view of an ovigerous female) 3 mm long, 3.2 times as long as wide, 0.2 times as deep as long. Pleotelson almost as broad as body width, as long as wide. Dorsum of body lacking setae. Pereonite 1 narrower and slightly longer than pereonites 2–4, not fused with head; pereonite 3 broadest in female, all of the same width in male; pereonites 5–7 of female slightly narrower, lateral margins slightly bent posteriorly; pleotelson smooth, with 2 shallow concavities at insertion of uropods.

Antenna 1 (Figs 10; 14) 0.2 body length in both sexes, of 8 articles in male (6 in female) more aesthetascs in male than in female. First article shorter than second, with some simple and broom setae; article 2 as long as 1, also with 4 broom and simple setae; article 3 slightly longer than 4, with lateral simple seta; article 4 with lateral and medial simple setae; article 5 longer than 4, articles 6 and 7 of male with 1 aesthetasc and 1 simple seta, (1 aesthetasc, 5 simple setae and 1 short broom seta in smaller female); article 8 (present in male only) with 1 aesthetasc, simple setae and a short broom seta.

Antenna 2 (Figs 10; 14) conjoint, of 23 articles in male (articles 1–4 broken off, not illustrated); article 2 of female (first not illustrated) short, quadrangular, without setation; article 3 of female 3 times as long as 2, with some simple

setae, antennal scale a lateral small spinulose spine; article 4 of female half as long as 3, with some simple setae; articles 5 and 6 of male about subequal in length, with lateral and medial simple setae, especially distally on 6; flagellar article 1 conjoint, with lateral and medial groups of simple long setae; following flagellar articles about subequal in length, with many long simple setae; last article with tuft of long simple setae.

Left mandible (Figs 10; 14) with 4 distinct cusps on incisor process in female (5 in male); right mandible with 5 in female (6 in male); lacinia mobilis shorter than incisor, with 4 cusps; left spine row with 6, right with 7 members; molar process broad, quadrangular, with medial indented grinding surface, posterior margin of molar with 4–5 lateral setae; condyle length 0.1 mandibular body length; palp article 1 shortest, article 2 slightly longer than 1; article 3 longest, slender, with 1–2 distal spines (article 3 broken off both mandibles of female), length of palp 0.7 mandibular body length.

Hypopharynx (Fig. 14) of 2 inner and 2 outer lobes, outer medially concave and covered with many short simple setae.

Maxilla 1 (Figs 10; 14) inner endite 0.4 width of outer endite; outer endite with 8–10 strong, smooth spine-like setae; inner endite with 3 strong simple setae and many slender simple ones (inner endite of female broken off).

Maxilla 2 (Figs 10; 14) innermost endite shortest, with 4–5 distal strong spine-like setae; medial and outer endites with 4 strong spine-like, medially serrated setae of varying lengths.

Maxilliped (Figs 11; 14) basis 2.7 times as long as wide, with 2 coupling hooks and 7–8 short fan-like setae distally, with lateromedial or distal (male) simple setae. Palp article 1 as long as last; article 2 broadest and longest; article 3 slightly shorter than 4; article 5 narrowest, with some apical simple setae. Epipod 3.7 times as long as wide, and 0.9 total basis length.

Pereopods (Figs 12; 15) bases length to body length ratio about 0.2 in both sexes. Pereopod 1 (Figs 12; 15) length 0.7 body length; carpus: basis ratio about 0.6; dactylus: propodus 0.5; dactylus with 2 simple short setae and 2 distal claws and 2 sensillae between; anterior claw about twice as long as posterior one. Pereopod 2 (Figs 12; 15) length 0.8 body length in both sexes. Carpus 0.7 basis length. Pereopod 3 (Figs 12; 15) length 0.8 body length in female. Carpus 0.8 basis length; dactylus length half of propodus length. Pereopod 4 (Figs 12; 15) length 0.8 body length in female. Carpus 0.8 basis length; dactylus length 0.4 propodus length. Pereopod 5 (Figs 12; 15) length of 0.9 body length in female. Carpus 0.9 basis length; dactylus length 0.4 propodus length. Pereopod 6 (Figs 12; 15) length 1.1 body length in female. Carpus as long as basis; dactylus length 0.4 propodus length. Pereopod 7 (Figs 12; 15) length 1.1 body length in female. Carpus as long as basis; dactylus length 0.4 propodus length.

Male pleopod 1 (Fig. 11) (precopulatory male) narrowing beyond four-fifths of length; length 4.2 times proximal width, distal width 0.5 proximal width; apex acuminating, with some short and 2 long setae.

Male pleopod 2 (Fig. 11) (precopulatory male), peduncle 2.1 times as long as wide; lateral margin slightly rounded, with 33 whip setae of different lengths and 5 distolateral plumose setae, which bear only few setules. Endopod inserting more proximally than halfway along; stylet slender, slightly longer than peduncle; 0.8 length of peduncle. Exopod small single lobe, without tuft of fine setae.

Female pleopod 2 (Fig. 16) anterior surface without setae, lateral margins surrounded with whip setae, distally with some plumose setae; 1.2 times as long as wide.

Pleopod 3 (Figs 11; 16) medial and lateral margins of exopod surrounded with fine setules. Endopod with 3 distal plumose setae, exopod slightly longer and more slender than endopod, distally with 5 plumose setae and laterally with fine setules. Pleopod 4 (Figs 11; 16) peduncle short, quadrangular; endopod slightly shorter than exopod and more slender; both rami without setae. Pleopod 5 (Figs 11; 16) an oval lobe without setae.

Uropod (Figs 11; 16) peduncle of male with spine-like structures; peduncle and rami with many long whip setae; peduncle and endopod not fused; endopod 0.54 as long as peduncle; exopod 0.9 endopod length.

Distribution. South-eastern Australia(35°–39°S); 115–520 metres depth.

Etymology. For HMAS *Kimbla* from which early sampling in Bass Strait was made.

Remarks. Ianthopsis kimblae can be distinguished from the other species of the genus by its much longer and broader pleotelson. *I. kimblae* is characterised by a rounded rostrum, much smaller than in other species. Most similar are *I. beddardi* (Studer, 1884) and *I. bovalli* (Studer, 1884), which can be distinguished from the new species by a longer rostrum. *I. beddardi* bears

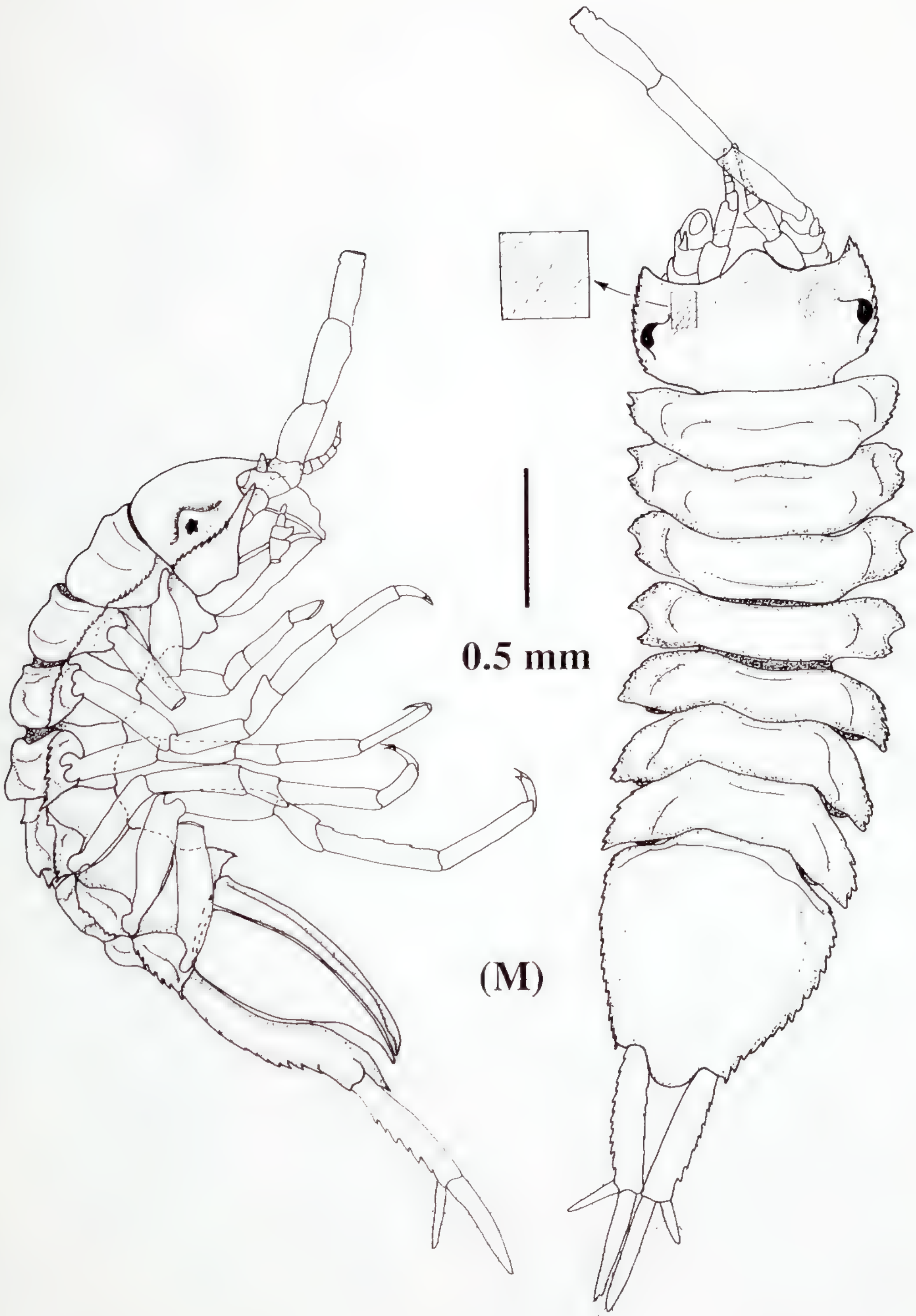

Figure 9. *Ianthopsis kimblae* sp. nov., holotype male in dorsal and lateral view; NMV J13271.

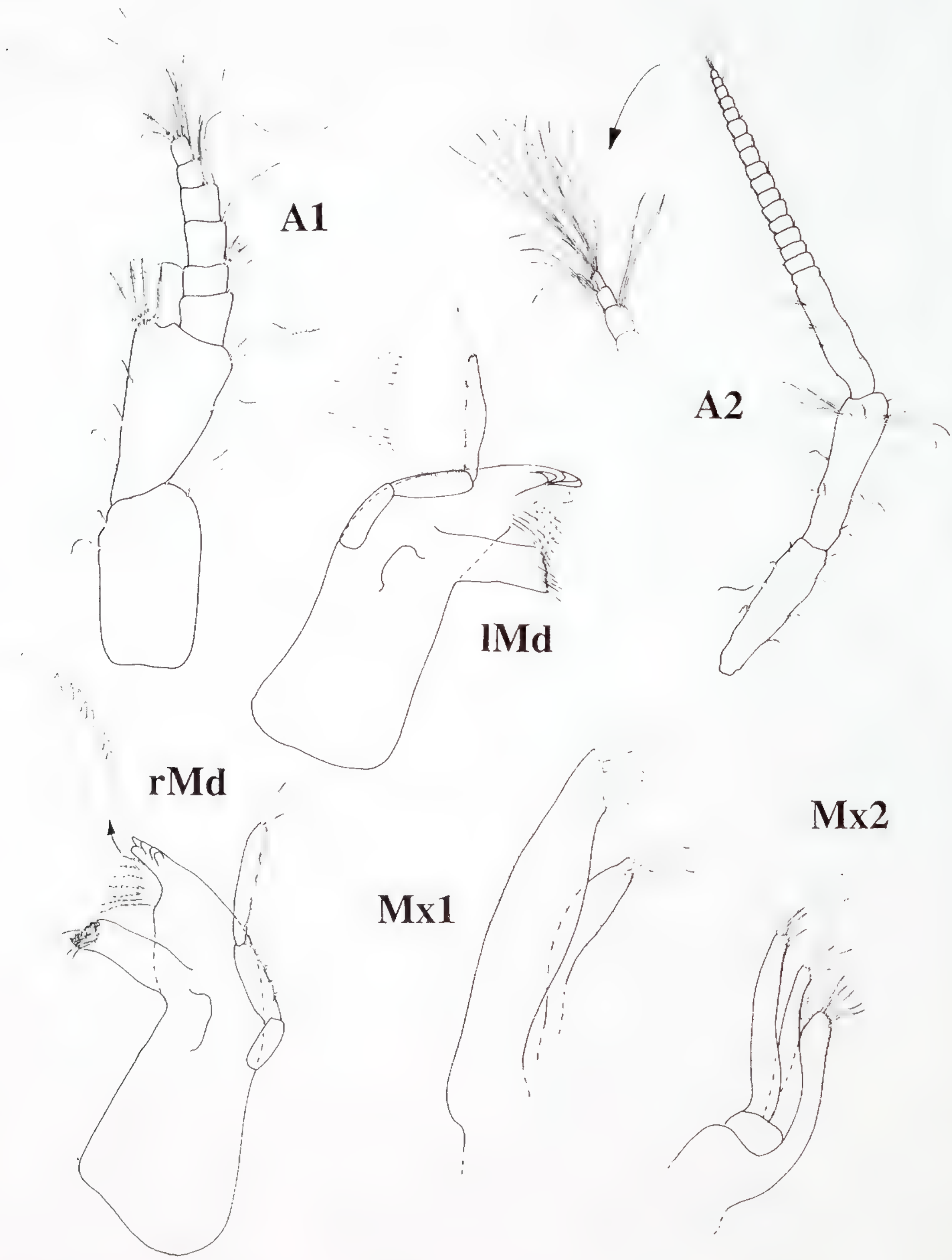

Figure 10. *Ianthopsis kimblae* sp. nov., paratype male, antenna 1, antenna 2 (proximal articles broken off), both mandibles, maxilla 1, maxilla 2; NMV J13272.

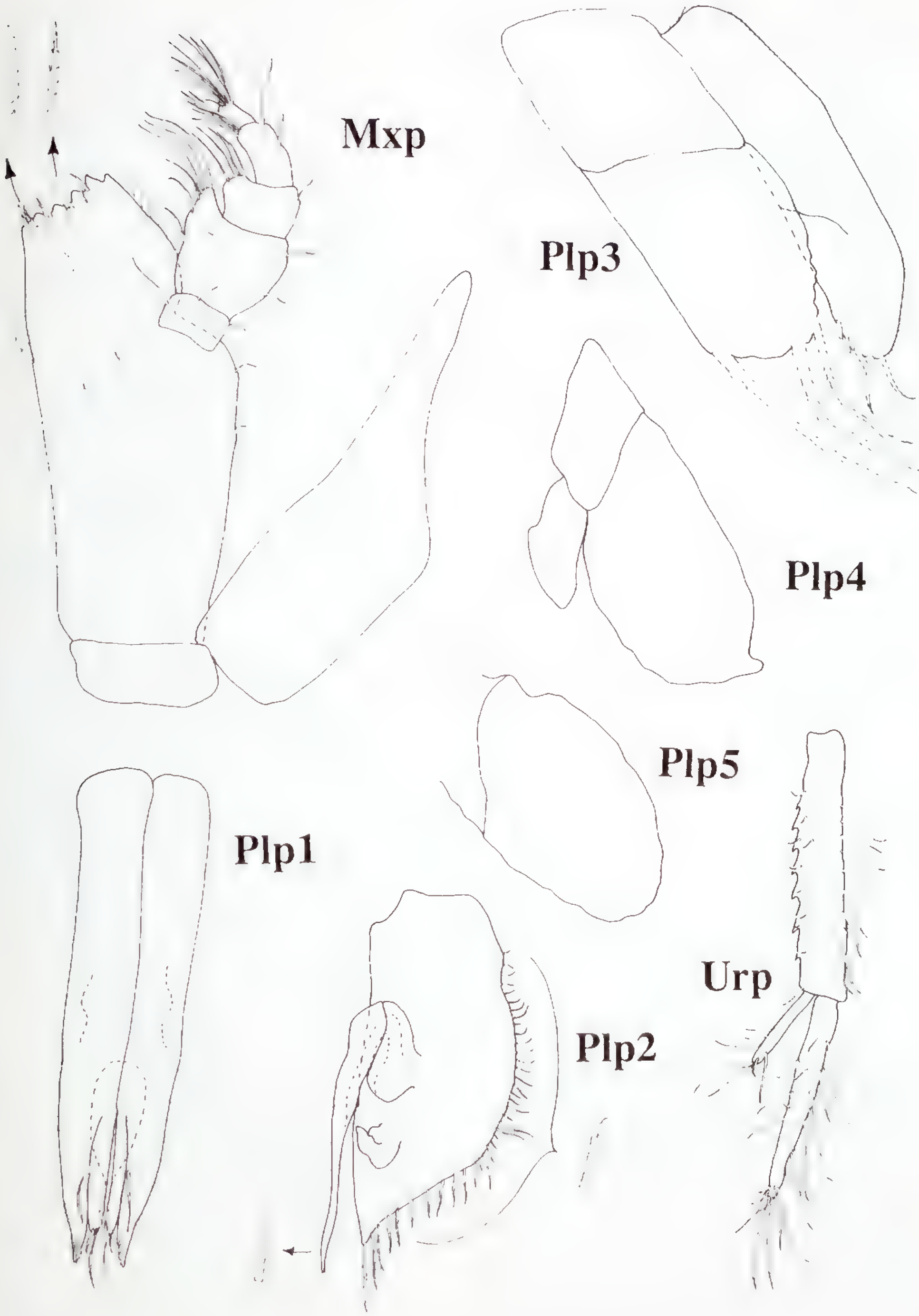

Figure 11. *Ianthopsis kimblae* sp. nov., paratype male, maxilliped, pleopods 1–5, uropod; NMV J13272.

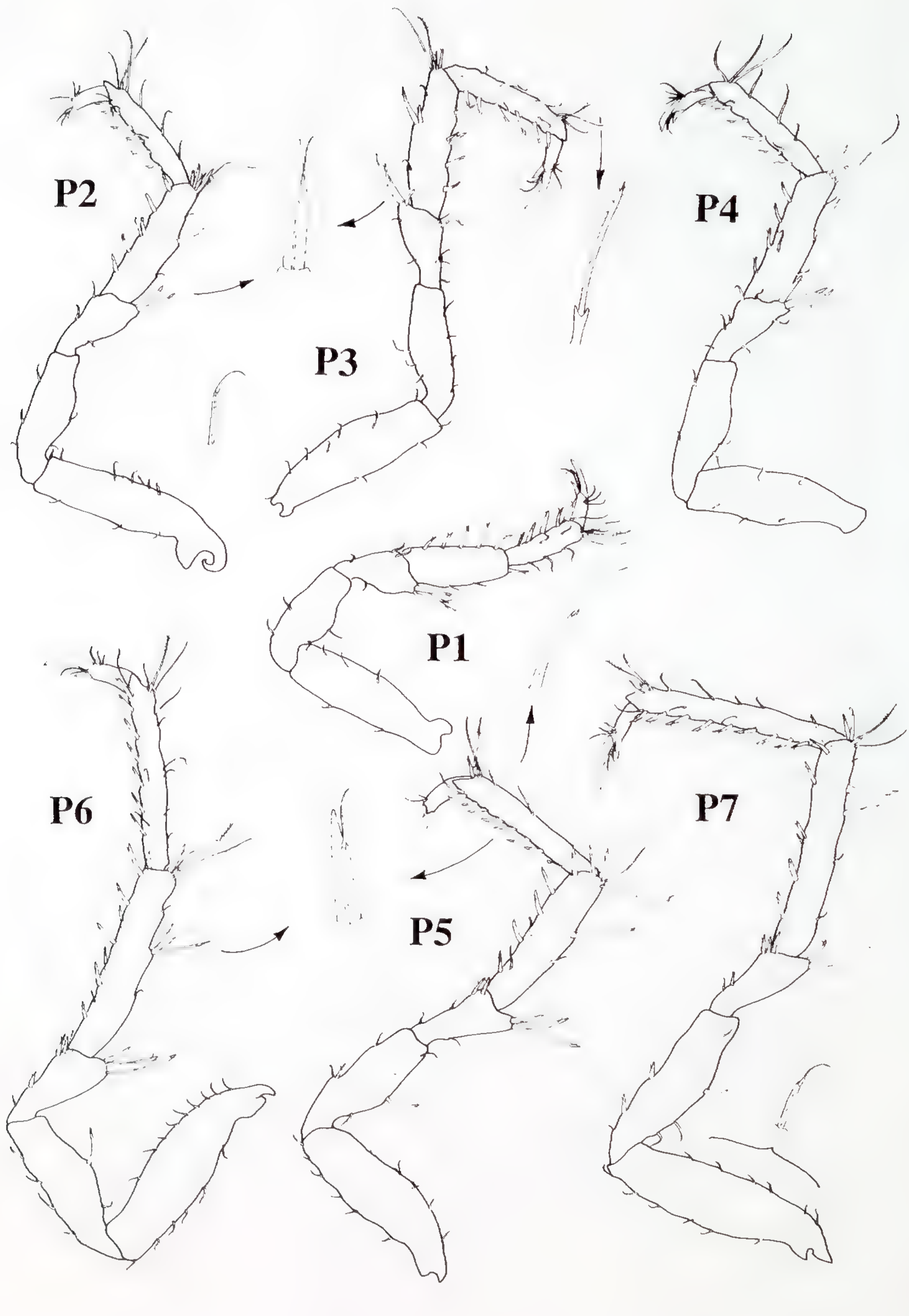

Figure 12. *Ianthopsis kimblae* sp. nov., paratype male, pereopods 1–7; NMV J13272.

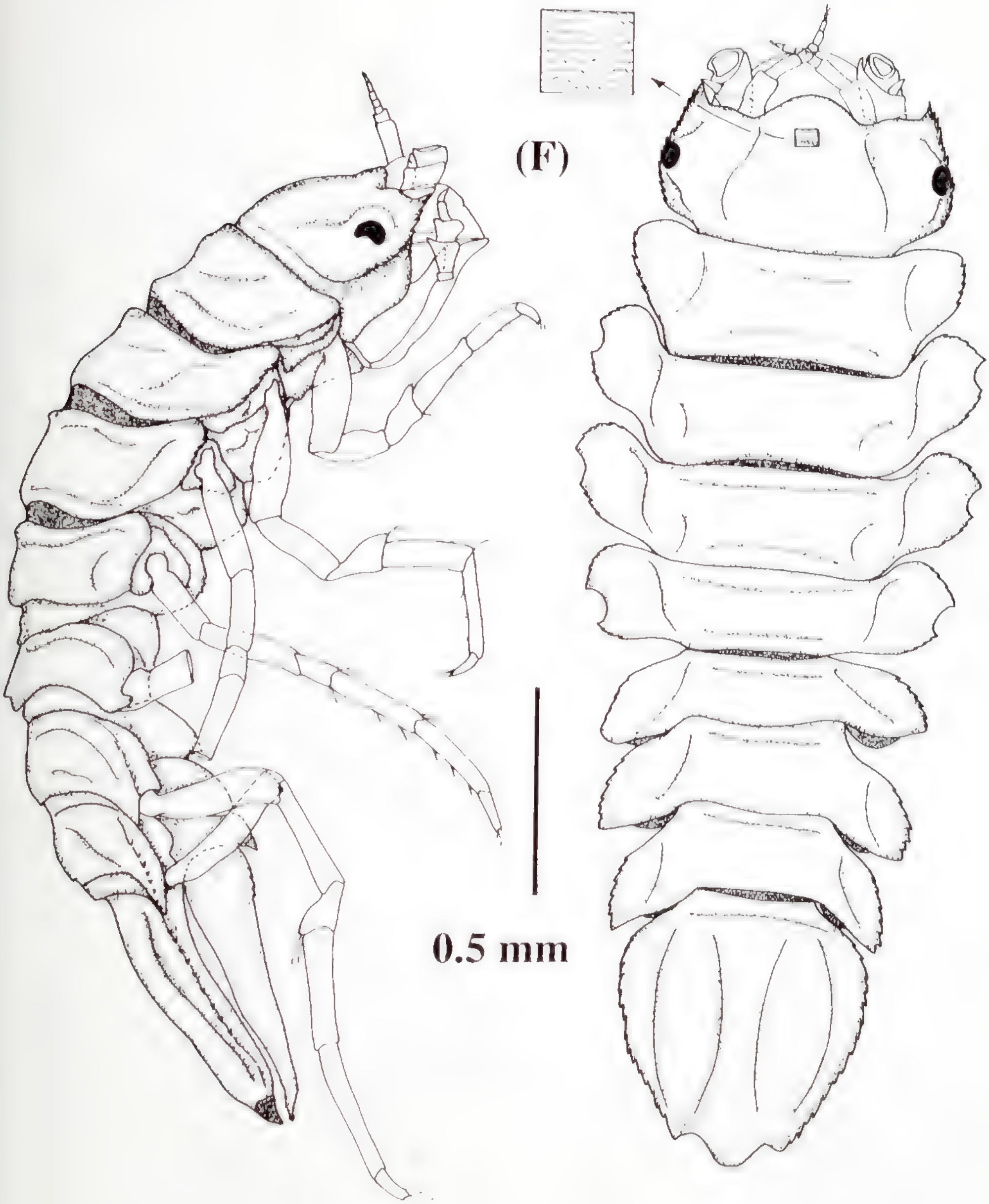

Figure 13. *Ianthopsis kimblae* sp. nov., allotype female in dorsal and lateral view; NMV J13272.

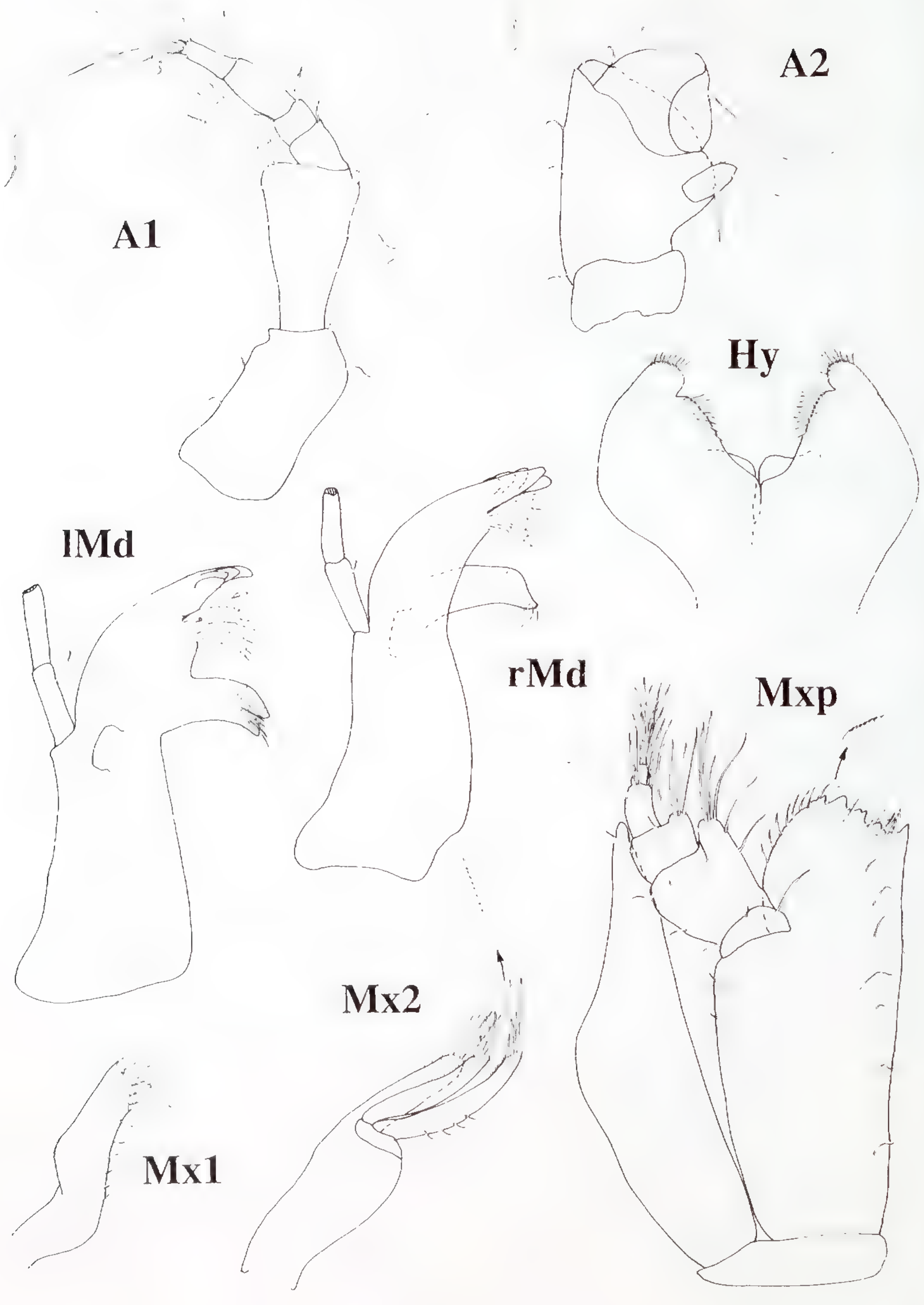

Figure 14. *Ianthopsis kimblae* sp. nov., paratype female, antenna 1, proximal articles of antenna 2, both mandibles, hypopharynx, maxilla 1, maxilla 2, maxilliped; NMV J13272.

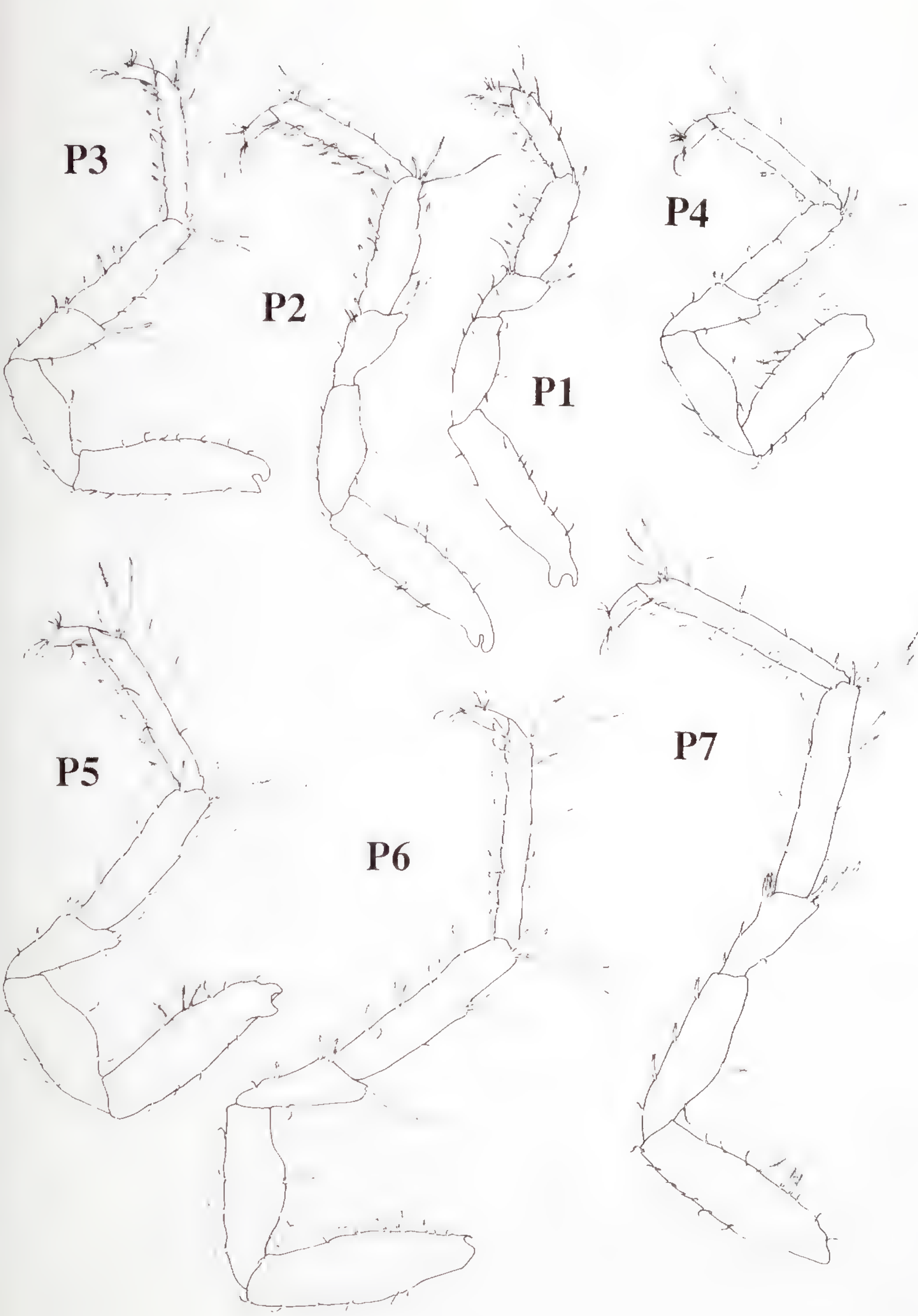

Figure 15. *Ianthopsis kimblae* sp. nov., paratype female, pereopods 1–7; NMV J13272.

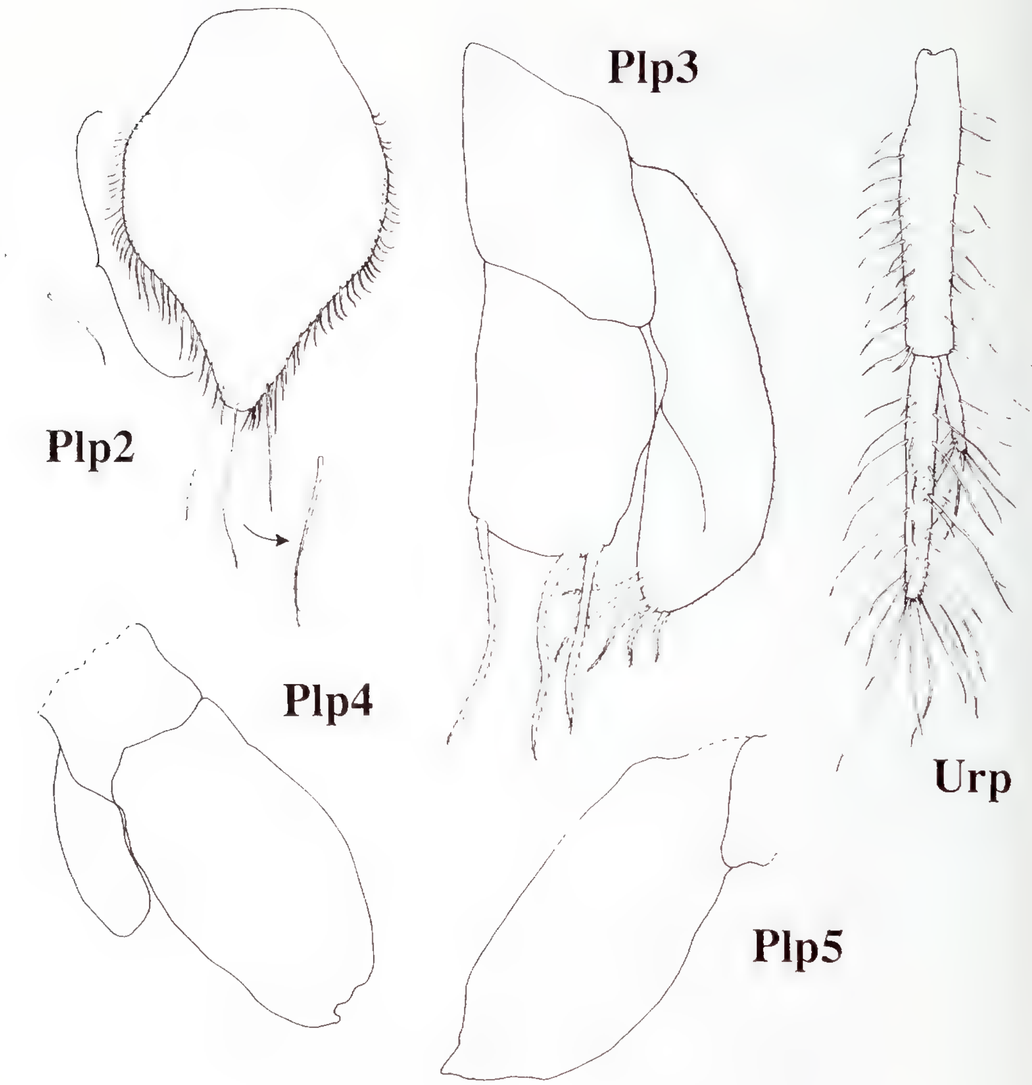

Figure 16. *Ianthopsis kimblae* sp. nov., paratype female, pleopods 2–5, uropod; NMV J13272.

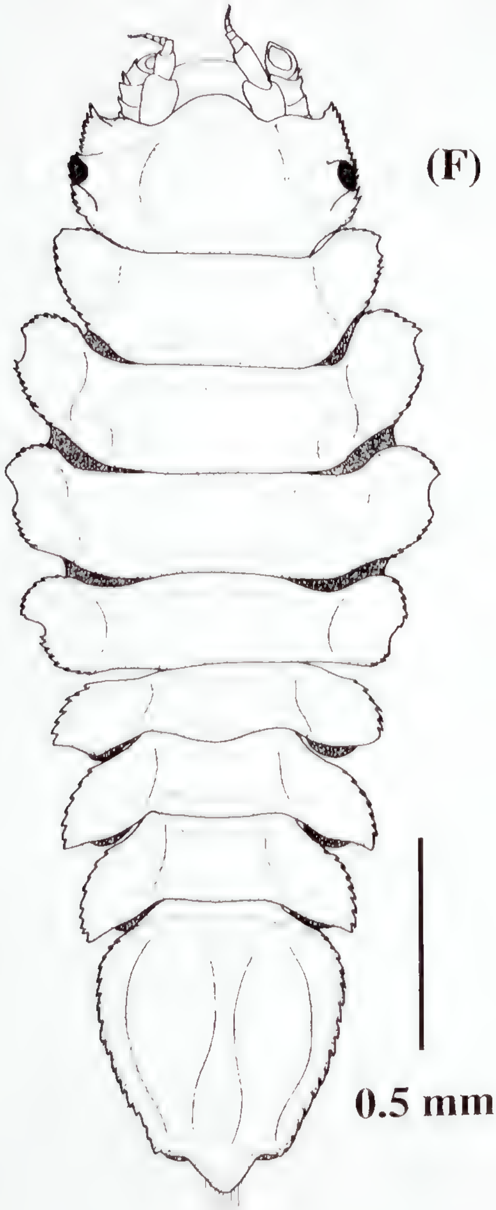

Figure 17. *Ianthopsis kimblae* sp. nov., paratype female, ovigerous specimen in dorsal view; NMV J13272.

small dorsal spines on all pereonites and *I. bovalli* has some spines on the first four pereonites whereas the new species is almost smooth except for low elevations. The other species with a smooth body surface have either a longer rostrum, like *I. ruseri* Vanhöffen, 1914 and *I. nodosa* Vanhöffen, 1914, or possess long setae on the dorsum, e.g. *I. laevis* Menzies, 1962.

Ianthopsis multispinosa Vanhöffen

Ianthopsis multispinosa Vanhöffen, 1914: 541–542. — Wolff, 1962: 258. — Kussakin, 1967: 340 [342]. — Brandt, 1991: 240–248, figs 24–29.

Material examined. Victoria, S of Point Hicks (38°25.9'S, 148°58.6'E), 1850m, muddy sandstone, 22 Jul 1986 (stn SLOPE 25), NMV J20172 (1); 76km S of Point Hicks (38°29.33'S, 149°19.98'E), 1840m, sandy mud, fine shell, 26 Oct 1988 (stn SLOPE 69), NMV J20173 (1), NMV J20174 (1) [both collected using WHOI epibenthic sled by G. C. B. Poore et al. on ORV *Franklin*].

Distribution. Gauss Station, Bellingshausen Sea, Antarctic Indian Ocean, Weddell Sea, Davis Sea; Australia, eastern Bass Strait, about 1850 metres depth.

Remarks. These records extend the distribution outside the Southern Ocean for the first time. Its distribution is best explained by continental drift vicariance.

No other species of this genus bears as long and acute spines as *I. multispinosa.*

Ianthopsis sp.

Material examined. Victoria, S of Point Hicks (38°14.8'S, 149°9.3'E), 200m, coarse sand, gravel (stn SLOPE 41), NMV J20194 (1); (38°17.7'S, 149°11.3'E), 400m, coarse sand, gravel, mud, many sponges (stn SLOPE 40), NMV J20193 (10), NMV J23844 (male A), NMV J23843 (female B) [both collected using WHOI epibenthic sled by M. F. Gomon et al. on ORV *Franklin*, 24 Jul 1986].

Distribution. Australia, eastern Bass Strait, 200–400 metres depth.

Remarks. This is almost certainly a new species with a spine pattern very similar to that in *Ianthopsis multispinosa*. Nevertheless, the new species is much smaller than *I. multispinosa* and its dorsal spines are shorter and more slender, even compared to juveniles. Two juveniles of 1.5mm length each, one male of 2mm length and 4 females of 2, 3, 2.6, and 3.2mm length have been found. The whole material is in too poor condition to describe.

Acknowledgements

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Memoirs of the Museum of Victoria 54:149–170 (1994)

REDESCRIPTION OF THREE POORLY KNOWN SPHAEROMATID GENERA (CRUSTACEA: ISOPODA) FROM SOUTH-EASTERN AUSTRALIA

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Abstract

Bruce, N.L., 1994. Redescription of three poorly known sphaeromatid genera (Crustacea: Isopoda) from south-eastern Australia. *Memoirs of the Museum of Victoria*. 54:149–170.

The genera *Cassidinella* Whitelegge, 1901, *Ceratocephalus* Woodward, 1877 and *Exocerceis* Baker, 1926 are rediagnosed. Their type species, *Cassidinella incisa* Whitelegge, 1901, *Ceratocephalus grayanus* Woodward, 1877 and *Exocerceis nasuta* (Whitelegge, 1902) are described in full. *Cassidinella akania* sp. nov. is also described and figured. The three genera are known only from south-eastern Australia between the central New South Wales coast to Tasmania and Victoria, with one record of *Ceratocephalus* from South Australia and one of *Exocerceis* from south-eastern Queensland.

Introduction

The sphaeromatid fauna of Australia is large, with in excess of 50 genera, and yet further genera undescribed. Of the named genera three, all endemic to south-eastern Australia, remain poorly characterised, not having been rediagnosed since their inception.

Ceratocephalus Woodward, 1877 is the first described endemic Australian sphaeromatid, and has the further distinction of being the only isopod named in the Encyclopaedia Britannica. The only Australian genera of greater antiquity than *Ceratocephalus* are widespread genera described by Leach (1815), Milne Edwards (1840) and the genus *Sphaeroma* Bosc, 1802. Surprisingly, as *Ceratocephalus* is not uncommon and is large by sphaeromatid standards, the genus was subsequently little recorded in the literature. *Cassidinella* Whitelegge, 1901, while provided with a detailed diagnosis by standards of that time remained equally poorly known. The third genus, *Exocerceis* Baker, 1926 was established for the species *E. nasuta* (Whitelegge, 1902). This genus is not common in benthic samples and, given the thorough surveys carried out in south-eastern Australia (e.g. Poore et al., in press), would appear to be restricted to central New South Wales and southern Queensland coasts.

Methodology and terminology follows that outlined in Bruce (in press). Abbreviations are as follows: AM, Australian Museum, Sydney; NMV, Museum of Victoria, Melbourne; NSW, New South Wales; SAM, South Australian Museum, Adelaide; PMS, plumose marginal setae; BL body length; imm, immature.

Sphaeromatidae Latreille

Sphaeromatinae Latreille

Ceratocephalus Woodward

Ceratocephalus Woodward, 1877: 659. — Beddard, 1886: 147. — Stebbing, 1893: 364. — Nierstrasz, 1931: 211.— Harrison, 1984: 375. — Harrison and Ellis, 1991: 935.

Bregmocerella Haswell, 1884: 1004.

Type species. Ceratocephalus grayanus Woodward, 1877, by monotypy (the genus name is correctly pronounced with a hard C, following its Greek derivation i.e. Keratokephalus).

Diagnosis of male. Body slightly less than twice as long as greatest width; widest at pereonite 5; dorsal surfaces rugose. Cephalon with projecting epistome; eyes lateral. Pereonites 2–4 coxae with posterior margin overlapped by next coxal plate; coxae of pereonite 5 overlapping those of pereonites 4 and 6; pereonite 7 narrower than 6. Pleon with 4 segments: segment 1 entire, 2–4 fused with sutures reaching to posterior margin. Pleotelson without entire exit channel, with apex produced. Pereonite 1 without sternite; pleonal sternite absent.

Antennule peduncle article 1 flattened, about as long (1.1) as wide, article 2 very short, about 0.3 as long as article 1 and 3, article 3 slender, nearly 10 times as long as wide; flagellum slightly shorter than peduncle. Antenna massive, enlarged, total length nearly as long as BL; antenna peduncle extending to pereonite 3, article 5 weakly reflexed against article 4, flagellum weakly reflexed against peduncle, with about 30 articles. Mandible unicuspidate, incisor blunt;

lacinia mobilis present on left mandible, spine row present, with 5–6 spines, molar prominent, gnathal surface smooth, marginal teeth present. Maxillule lateral lobe with gnathal spines simple, mesial lobe with 2 serrate and 2 (lateralmost) weakly plumose spines. Maxilla lateral and middle lobe entire, mesial lobe slender, with serrate spines. Maxilliped palp articles 2, 3 and 4 with strongly setose lobes on mesial margin, article 5 elongate; endite distal margin with about 10 weakly serrate spines, 4 submarginal spines 3 spines on dorsal distomesial margin.

Pereopod 1 robust, ambulatory, posterior margin of merus, carpus and propodus with stout acute spines; dactylus with prominent simple accessory unguis. Pereopods 2–7 slender; pereopods 2–6 subsimilar, merus and carpus posterior margin with setulose fringe, merus, carpus and propodus with acute spines; spines longer on pereopod 6; pereopod 7 more slender than 6, without spines, propodus flattened, distally expanded, posterior margin with dense setulose fringe, dactylus short less than half (0.46) length of propodus.

Penes basally close set, not fused, elongate, about 8 times as long as basal width, distal half slender.

Pleopod 1 endopod mesial margin with recessed groove (which receives appendix masculina); distally narrowed forming triangular shape with proximolateral angle produced. Pleopod 2 similar to 1 in shape, appendix masculina slender elongate, about 1.4 times as long as endopod. Pleopod 3 exopod with entire transverse suture. Pleopods 1–3 with both rami with PMS. Pleopod 4 exopod with transverse suture, mesial margin with simple marginal setae; endopod with prominent deep ridges on dorsal side. Pleopod 5 exopod with transverse suture, mesial margin with simple marginal setae, distal margin subtruncate, thickened, covered with scales, mesial margin with 2 scaled lobes adjacent to suture, third prominent scaled lobe positioned about two-thirds along mesial margin; endopod with prominent deep ridges on dorsal side only. Uropod with small exopod set in ventrolateral position into lateral excision; endopod not extending beyond pleotelson apex.

Female. Similar to male, but lacking cephalic ornamentation, epistome not anteriorly produced; pereopod 7 similar to pereopod 6. Ovigerous females with mouthparts metamorphosed; oostegites arising from coxae of pereopods 1, 2, 3 and 4 and overlapping at midline. Embryos held within body cavity, visibly packed into cephalic space. Ovigerous females with noticeably thinner cuticle then males.

Remarks. Adult males of the monotypic genus *Ceratocephalus* are readily recognized by the elongate cephalic process which, with the elongate and upturned epistome, give a tricorn appearance. No other sphaeromatid genus has antennae as enlarged as those of *Ceratocephalus*. The cephalic ornamentation is not included in the generic diagnosis as such ornamentation is often not of generic value within the Sphaeromatidae.

Ceratocephalus belongs to a group of genera, all of which have a rugose body appearance, and have pereonite 5 overlapping pereonites 4 and 6; additionally these genera also have the posterior margins of pereonites 2 and 3 overlapped by the anterior margin of the next coxae, the reverse of that which is more usual. These genera are *Caecocassidias* Kussakin, 1967, *Kranosphaera* Bruce, 1992, *Moruloidea* Baker, 1908 and *Waiteolana* Baker, 1926.

Although *Cymodopsis wardii* Baker, 1926 is a junior synonym of the type species of *Ceratocephalus* the two genera are not readily confused. All species of *Cymodopsis* Baker, 1926 have the coxae overlapping anterior to posterior.

Iverson (1982) stated that *Bregmocerella* was a preoccupied name while earlier Whitelegge (1902) believed *Ceratocephalus* was preoccupied. *Ceratocephalus* and *Ceratocephala* (a trilobite) are not homonyms, and *Ceratocephalus* Woodward, 1877 is the senior objective synonym.

Ceratocephalus grayanus Woodward

Figures 1–6

Ceratocephalus grayanus Woodward, 1877: 659, fig. 72. — Stebbing, 1893: 356, fig. 31. — Beddard, 1886: 148.— Nierstrasz, 1931: 211.

Bregmocerella tricornis Haswell, 1885: 1004, pl. 53, fig. 1. —Stebbing, 1893: 365. — Whitelegge, 1902: 274.

Cymodopsis wardii Baker, 1926: 267, pl. 46 fig. 12, pl. 47 figs 1–2.

Material examined. New South Wales. 3♂ (17.9, 19.5, imm. 12.9 mm), 4 imm. (8.4, 8.7, 12.3, 12.6), E of Malabar, 33°57'S, 151°19'E, 2 Jan 1973, 32 m, coll. AMSBS (AM P22227). 3♂ (imm. 11.2, 12.6, 15.4 mm), 2♀ (ovig. 16.1, non-ovig. 16.8 mm), imm. (10.9, 11.2 mm), same location (AM P22229). 3♂ (18.2, 18.9, 19.5 mm), ♀ (ovig. 15.4 mm), imm. (12.5, 13.7 mm), same location but 1973, depth not recorded (AM P22228). 3♂ (imm. 9.8, 10.5, 12.6 mm), ♀ (ovig. 15.4 mm), imm. (8.4, 9.1 mm), E of Long Reef, 33°43'S, 151°46'E, 20 Dec 1985, 174 m, J. K. Lowry and R. T. Springthorpe on FRV *Kapala* (AMP41854).

Additional material. ♀ (non-ovig.), 64km SW of Mt Cann, Vic., 36m, F.I.S. *Endeavour* Expedition, 1909–1914 (AM E6756). ♂ (very poor condition), 4km offshore Newcastle Bight, NSW, 32°50'S, 152°03.5'E, 7 Mar 1898, 46m, sand and pebbles, E. R. Waite on H.M.C.S. *Thetis* (AM G2215). ♂ (dissected, intact), 3km E of Cape Three Points, NSW, 33°30'S, 151°27'E, 22 Feb 1898, 50m, brown sand, E. R. Waite on H.M.C.S. *Thetis* (AM G2198). Imm., off Wineglass Bay, Tas., 42°10'S, 148°18'E, no date, 146m, E. A. Briggs (AM P10708).

New South Wales. Imm., off Port Stephens, 32°52'S, 152°32'E, 144m (AM P41312). 6 mancas (3.5–4.2mm), off Newcastle, 32°53'S, 152°35'E, 175m (AM P41315). Manca (6.3mm), off Sydney, 33°46'S, 151°43'E, 176m (AM P41321). ♀ (ovig.), manca, off Stanwell Park, 34°13.8'S, 151°29.1'E, 466–498m, W. Ponder and R. T. Springthorpe on FRV *Tangaroa* (AM P41307) 6 ♀ (2 ovig), off Port Hacking, 34°11.1'S, 151°26.0'E, 198m (AM P41308).

Victoria: ♂, 34km S of Lake Tyres Entrance, 38°11'S, 148°04'E, 56m, clean shell rubble (NMV J26260). Western Port: ♀, 38°19.92'S, 145°13.95'E, 19m, sand, gravel (NMVJ2929); ♂, 38°26.45'S, 145°21.93'E, 6m, sand (NMV J2930); ♂, mancas, 38°26.64'S, 145°18.79'E, 14m, sand (NMV J2931); ♂, 38°21.35'S, 145°13.36'E, 10m (NMV J26373). ♂, 7 imm. and mancas 38km SW of Cape Paterson, 38°55.5'S, 145°17.0'E, 70m, fine sand (NMV J31524, J26413). ♀, 43km SW of Port Albert, 38°53.7'S, 147°06.5'E, 58m, coarse shell (NMV J31525).

Tasmania: 4 ♀, 40km NNE of Deal I., 39°06'S, 147°26'E, 59m, clean shell rubble (NMV J26254).

South Australia: ♀ (ovig), Pearson I., Investigator Group, 26 Jun 1973 (SAM C4357).

Holotype of *Cymodopsis wardii* Baker, in very poor condition, pleon and pleotelson missing, 26–29km NE of South Head, Port Jackson, NSW, 33°44'S, 151°34'E, May 1924, 142–146m, C. E. Mulvey on *Goonambee* (AM P9494).

Type locality. Stated by Woodward (1877) to be Flinders Island, Bass Strait.

Types. Apparently not held at the BMNH, as they are absent from the list of types given by Ellis (1981). Similarly Haswell's (1885) specimens no longer appear to be extant as no record of them exists at the Australian Museum, and all efforts to trace the specimens have been without success (pers. comm., R. T. Springthorpe, AM).

Description of male. Body about 1.6 times as long as wide (excluding epistome), widest at pereonite 5. Cephalon dorsal surface obscurely bidomed, with tubercles and pits; eyes set on prominent ocular bulge, facets distinct; 2 long (23% BL) subocular horns present anterior to eyes, bending laterally at about two thirds of their length. Pereonite 1 with 2 sublateral patches of thickened and ridged cuticle; pereonites 2–6 with transverse ridge on posterior half; pereonite 7 with posterior margin weakly produced. Pleon posterior margin and dorsal surfaces tuberculate. Pleotelson strongly vaulted, bidomed, with prominent tubercles on dorsal surface.

Epistome produced forming elongate upwardly curving process, about 58% BL (in lateral view). Antennule peduncle article flattened, about as long as wide, article 2 short, about 0.3 as long as 1; article 3 slender about 9 times as long as wide; flagellum with about 29 articles, slightly shorter than peduncle.

Mandible palp slender, article 2 with about 10 biserrate setae on distolateral margin, lateral margin of article 3 with 27 biserrate setae and 3 distal setae which are twice as long as others. Maxillule lateral lobe with 11 long and 2 short spines. Maxilla lateral and middle lobes with 8 setae each, mesial lobe with serrate spines in 2 ranks of 8 and 9 each.

Pereopod 1 merus, carpus and propodus with 5, 4 and 6 spines respectively; posterior margins of ischium to propodus without dense setulose fringe. Pereopod 2 posterior margin ischium, merus and carpus each with 4, spines.

Pleopod 1 exopod and endopod with about 76 and 34 PMS respectively; exopod with prominent spine at proximolateral angle; surfaces of peduncle and mesial portion rami setulose. Pleopod 2 exopod and endopod with about 80 and 36 PMS respectively; appendix masculina about 1.6 times as long as medial length of endopod. Uropod dorsal surface tuberculate; distal margin obliquely truncate, distolateral margin concave, with prominent tubercle, midlateral margin irregularly excavate, with exopod set into anterior portion of excavation; exopod small, 0.2 length of endopod, distally acute.

Female. Epistome anterior margin projecting and narrowed, but not extending beyond anterior margin of cephalon, otherwise as for the generic diagnosis.

Colour. Pale tan to cream in alcohol; chromatophores present on appendages.

Size. Mature males (with developed cephalic processes and epistome) about 17 to 20mm; ovigerous females 15.4 to 16.1mm, immature males recognisable at 9.8 to 15.4mm, and mancas 3.5 to 6.3mm.

Distribution. Eastern coast of New South Wales from Newcastle Bight (32°50'S) to Wineglass Bay, Tasmania (42°10'S), and westwards to Pearson I., South Australia at depths from 6m in enclosed bays such as Western Port, Victoria, to between 32 and 498m offshore.

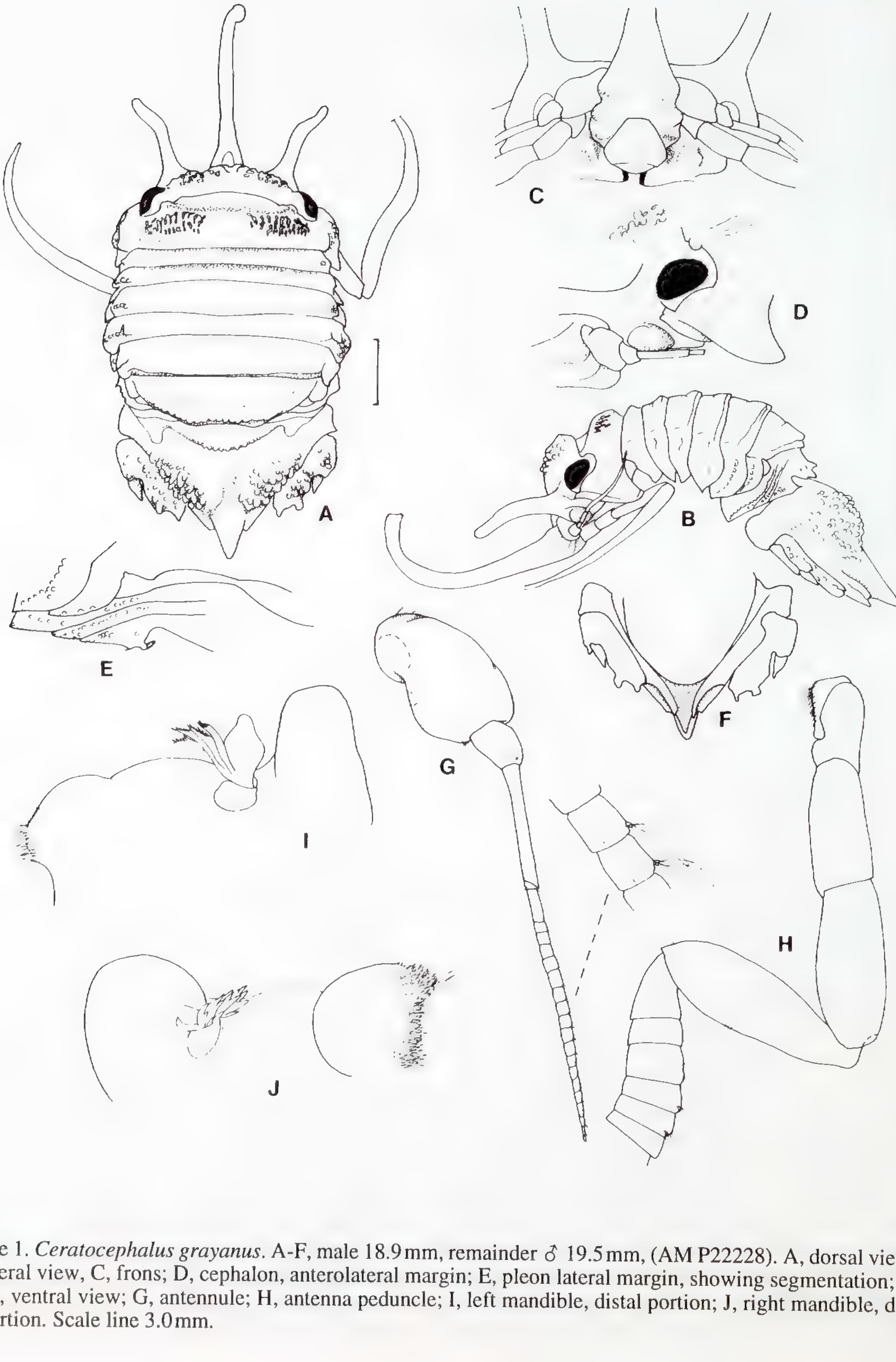


Figure 1. *Ceratocephalus grayanus*. A-F, male 18.9 mm, remainder ♂ 19.5 mm, (AM P22228). A, dorsal view; B, lateral view, C, frons; D, cephalon, anterolateral margin; E, pleon lateral margin, showing segmentation; F, pleon, ventral view; G, antennule; H, antenna peduncle; I, left mandible, distal portion; J, right mandible, distal portion. Scale line 3.0 mm.

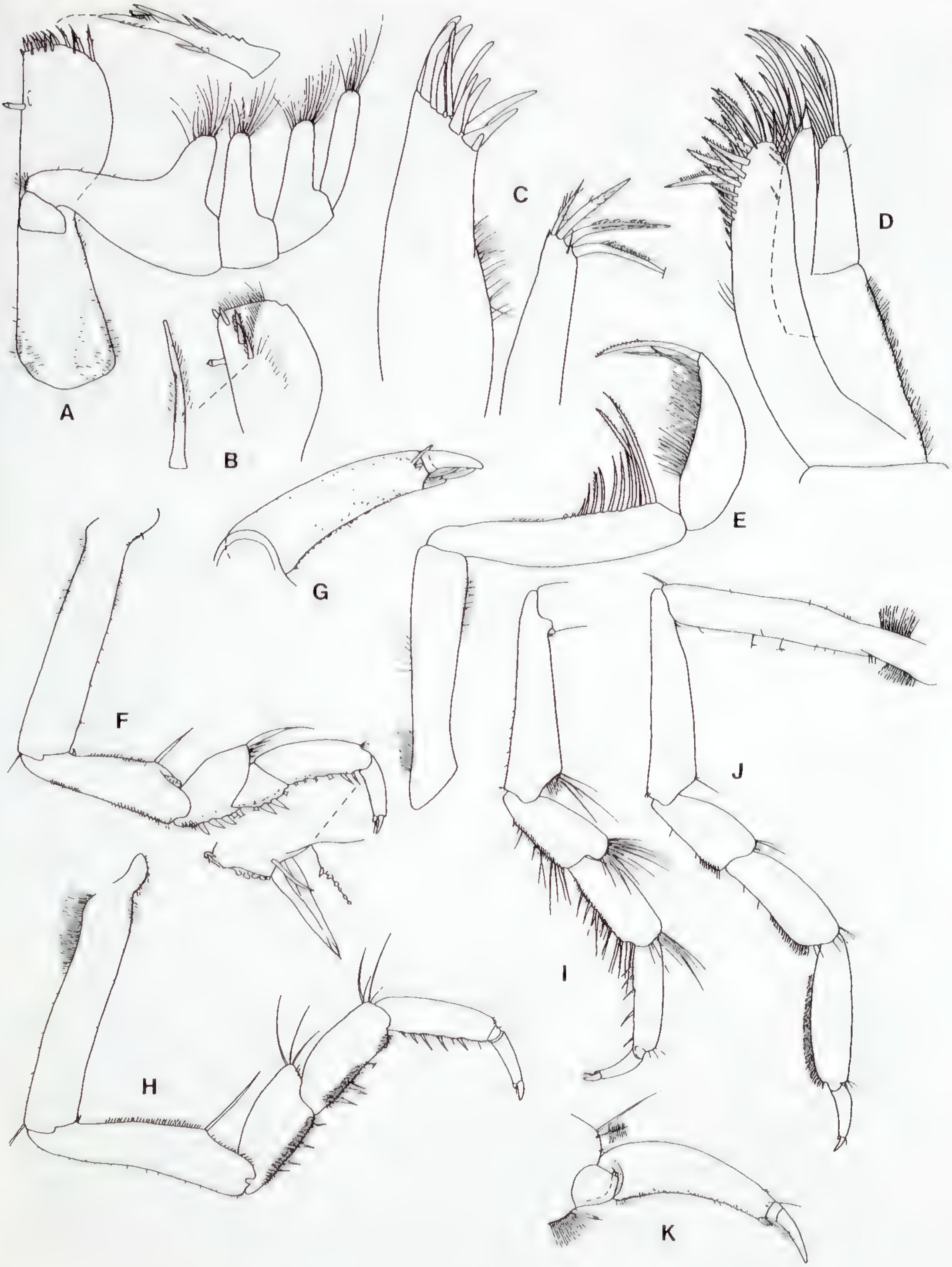


Figure 2. *Ceratocephalus grayanus*. All figs ♂ 18.9 mm (AM P22228). A, maxilliped; B, maxilliped endite, dorsal surface; C, maxillule; D, maxilla; E, mandible palp; F, pereopod 1; G, pereopod 1 dactylus; H, pereopod 2; I, pereopod 6 (basis omitted); J, pereopod 7; K, pereopod 7, dactylus.

Remarks. Adult males are impossible to confuse with any other sphaeromatid. The shape and ornamentation of the pleotelson, which has an acute apical projection over the sinus, and of the uropods, which have a large endopod not extending beyond the posterior margin of the pleotelson and a small, acute exopod set in a ventrolateral position, allow identification females and juveniles.

The description is based primarily on specimens from East of Malabar (AM P22228, P22229).

Cassidinella Whitelegge

Cassidinella Whitelegge, 1901: 241. — Nierstrasz, 1931: 211. — Harrison, 1984: 374. — Harrison and Ellis, 1991: 934.

Type species. Cassidinella incisa Whitelegge, 1901, by monotypy.

Diagnosis of male. Body strongly vaulted. Cephalon with rostral point in ventral position; eyes round, facets distinct, set on short lobe. Pereonite 1 longest, 2–6 subequal in length; coxae ventrally produced, distally acute. Pleon with 4 segments, segment 1 entire, 2 separate sutures running to posterior margin. Pleotelson strongly vaulted, posteriorly without foramen or ventral exit channel; posterior margin with 3 pointed coplanar lobes. Pereonite 1 without sternal extensions; pleonal sternite absent.

Epistome shorter than wide, with apical point, not extending between antennule bases. Antennule peduncle robust, with 4 articles, flagellum shorter than peduncle. Antenna slender,

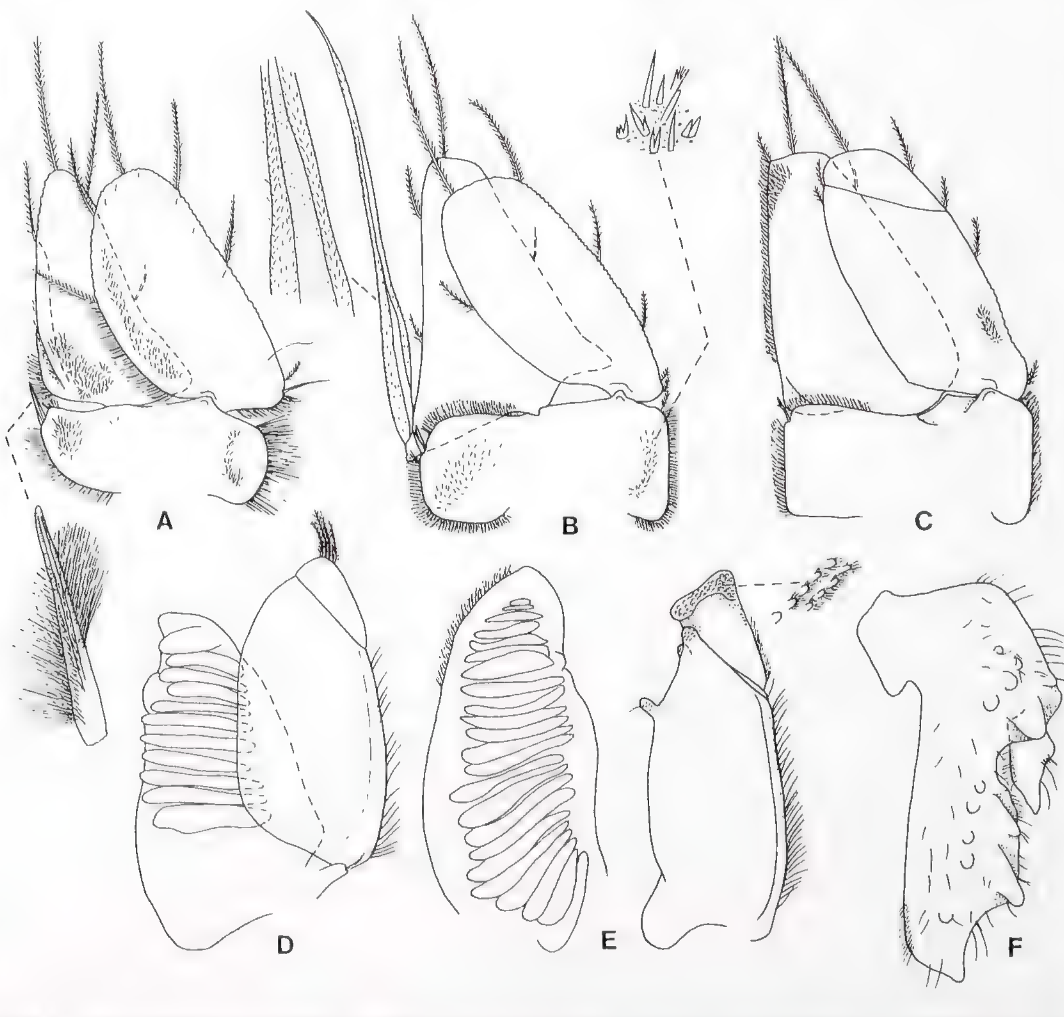


Figure 3. *Ceratocephalus grayanus.* All figs ♂ 18.9 mm (AM P 22228). A-E, pleopods 1–5 respectively; F, uropod.

peduncle articles 1–3 short, article 5 longest, flagellum and peduncle subequal in length. Mandible incisor unicuspidate oblique; tridentate lacinia mobilis prominent on left mandible; spine row of 5 sub-bifid spines; molar process with abundant marginal teeth, mesial surface shallow, concave, irregular. Maxillule mesial lobe with 4 fringed spines, lateral lobe with 11 stout weakly serrate spines. Maxilla entire, setae on lateral and middle lobe finely pectinate. Maxilliped palp articles 2–4 mesial margins with elongate lobes; endite distal margin subtruncate with slender circumplumose spines, single smooth spine at distomesial angle.

Pereopods all ambulatory, dactylus with short acute accessory spine; pereopod 1 robust, with stout spines on posterior margin, pereopods 2–6 subsimilar, pereopod 7 slender.

Penes set well apart, unfused, distally narrowed.

Pleopods 1–3 with PMS on both rami, pleopods 4 and 5 without PMS. Pleopod 1 endopod triangular, exopod distally rounded, peduncle about 2.5 times as wide as long. Pleopod 2 endopod triangular in shape; appendix masculina basally attached. Pleopod 3 endopod triangular in shape, exopod with prominent transverse suture. Pleopod 4 endopod with transverse thickened ridges, single distal seta; exopod with transverse suture. Pleopod 5 endopod with ridges not strongly developed; exopod with transverse suture; lateral margin with row of simple setae, mesial margin with cuticular scales and 4 scaled lobes, 2 distal to suture, 2 proximal to suture.

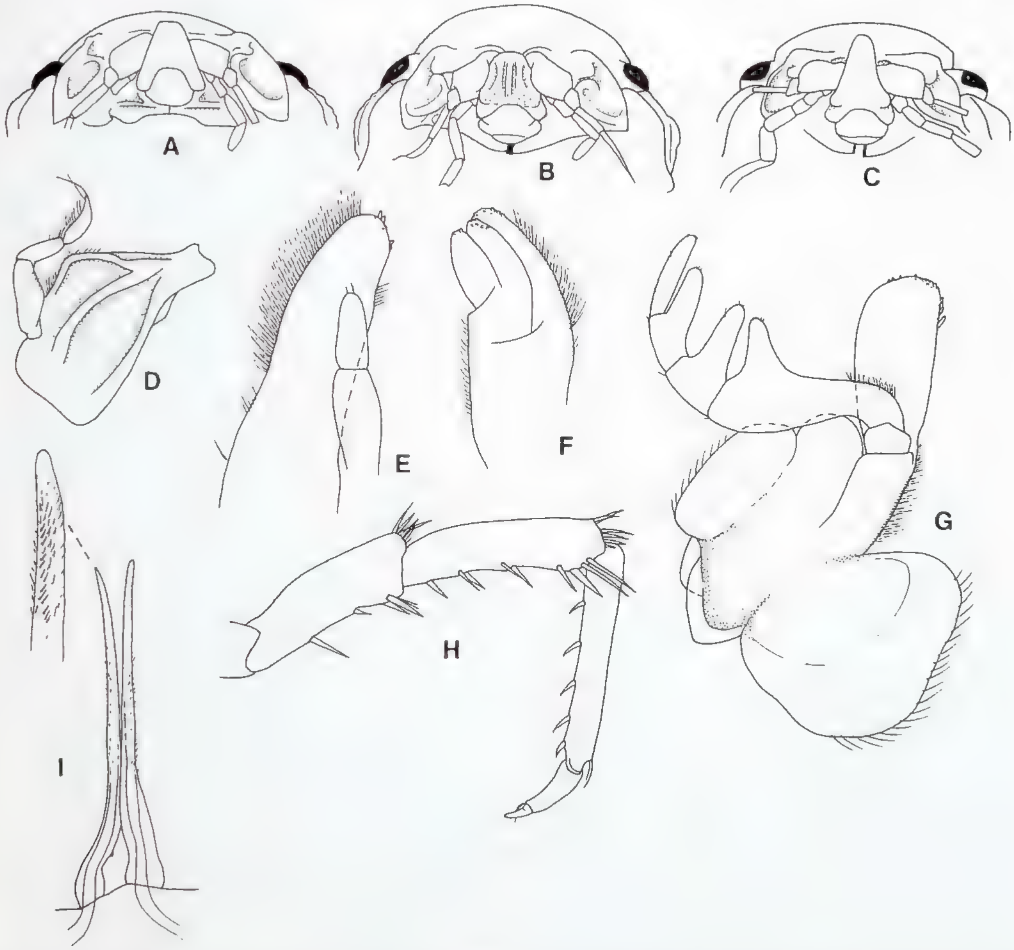
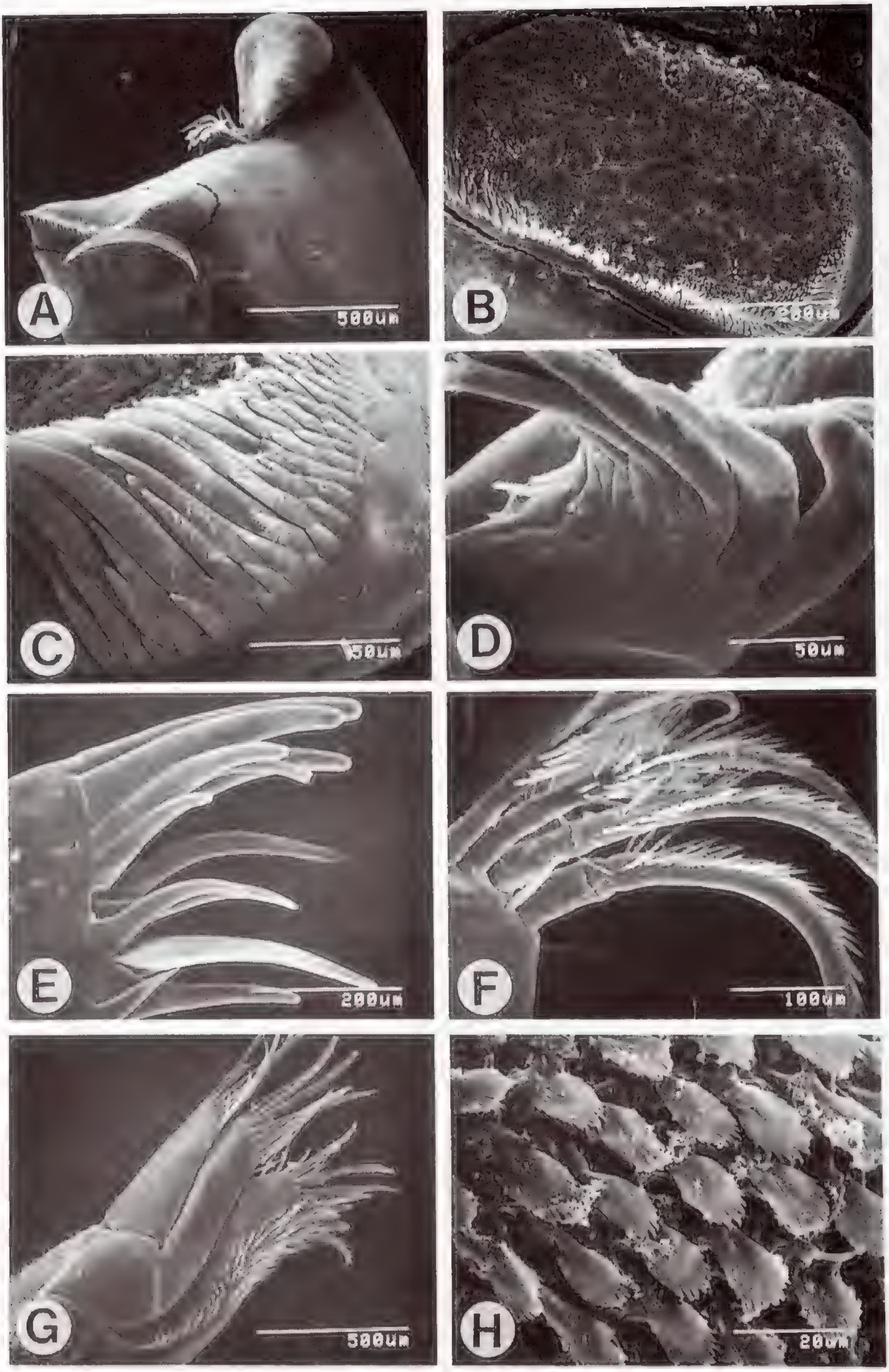


Figure 4. *Ceratocephalus grayanus*. A, D–H, ovig. ♀ 16.1 mm, remainder as indicated (AM P22229). A, frons; B, non-ovig. ♀ 16.8 mm, frons; C, imm. male 15.4 mm, frons; D, mandible; E, maxillule; F, maxilla; G; maxilliped; H, pereopod 7, distal articles; I, penes, male 18.9 mm (AM P22228).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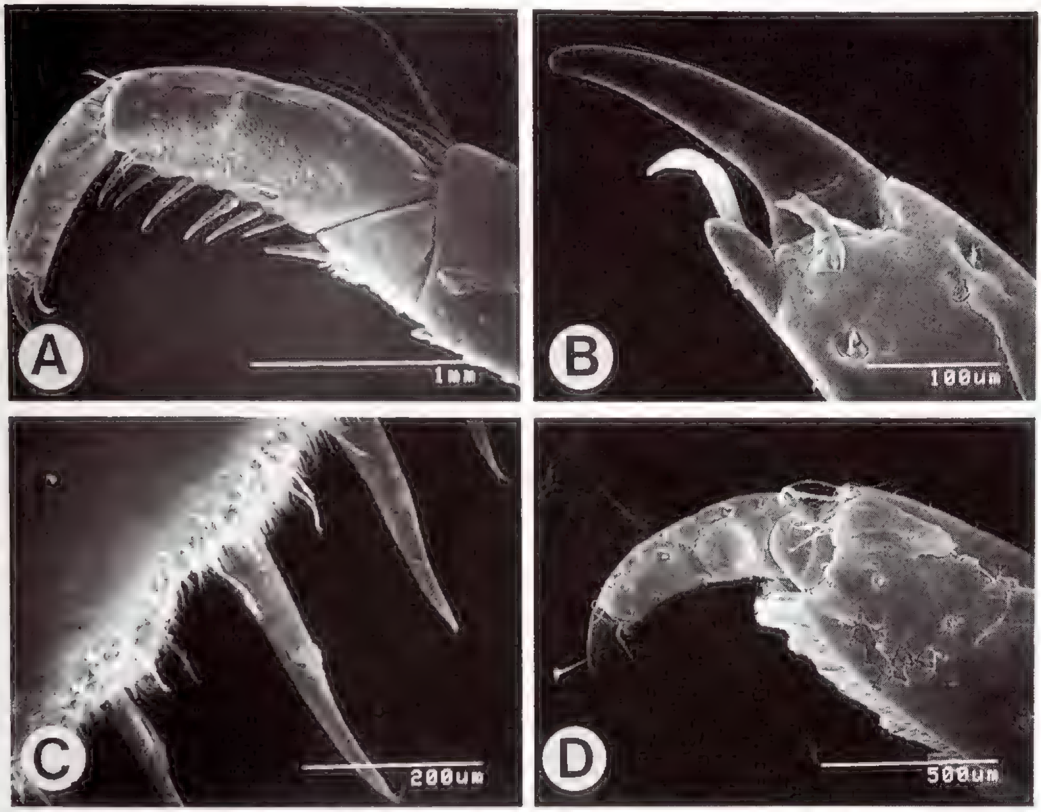

Figure 6. *Ceratocephalus grayanus*. ♂ AM P22228. A, pereopod 1; B, pereopod 1, unguis; C, setules and spines, pereopod 2 merus; D, pereopod 7 distal propodus and dactylus.

Uropod endopod not reaching pleotelson apex exopod small, about half as long as endopod.

Female. Ovigerous females not present in material examined.

Composition. The type species and *Cassidinella akania* sp. nov. described here.

Remarks. The morphology of the coxae, pleon lateral margin (both distally acute) and the pleotelson posterior margin being formed into three prominent coplanar points readily separates *Cassidinella* from all other sphaeromatine genera.

The two species show considerable differences in ornamentation *C. incisa* having a smooth cuticle, while *C. akania* sp. nov. is covered in spines and setae; the antennule peduncle of *C. incisa* is not flattened while that of *C. akania* is strongly flattened with a falcate second article, and is very similar in appearance to the antennules of such genera as *Platysphaera* Holdich and Harrison and *Syncassidina* Baker (see Bruce, 1994); pereonite 7 in *C. incisa* is shorter and narrower than pereonite 6, while pereonite 7 of *C. akania* is as wide and as long as pereonite 6.

←

Figure 5. *Ceratocephalus grayanus*. ♂ AM P22228. A, right mandible, distal margin; B, molar, *en face*; C, molar, proximal spines; D, spine row; E, maxillule, lateral lobe; F, maxillule, mesial lobe; G, maxilla; H, pleopod 5, scale patch.

Key to species of *Cassidinella*

1. Body smooth; cephalon, pereonite 1, pleon and pleotelson without acute bosses; antennule peduncle articles 1 and 2 not flattened .... *C. incisa*
— Body with abundant setae and spines; cephalon, pereonite 1, and pleotelson with 2 acute submesial bosses, pleon with 1 median boss; antennule peduncle articles 1 and 2 strongly flattened .... *C. akania*

Cassidinella incisa Whitelegge

Figures 7–10

Cassidinella incisa Whitelegge, 1901: 242, figs 23a–g. — Baker, 1926: 269. — Nierstrasz, 1931: 211.

Material examined. Holotype. ♂ (7.3 mm, previously dissected and microslide), 2 km E of Orient Point, NSW, 34°13'S, 150°48'E, 20 Mar 1898, 20–27 m, sand and rock, E. R. Waite on H.M.C.S. *Thetis* (AM G2402).

Other material. New South Wales. 2♀ (non-ovig. 7.4, damaged 8.0 mm), off Broken Bay, 33°34'S, 151°41'E, 10 Feb 1986, 135 m, FRV *Kapala* (AM P41316). 2♂ (6.0, 6.3 mm) ♀ (8.4 damaged), E of Long Reef, 33°43'S, 151°46'E, 20 Dec 1985, 174 m, J.K. Lowry and R. T. Springthorpe, F.R.V. *Kapala* (AM P41025, P41853). ♂ (c. 5.4 mm, 2 broken), 26–29 km NE of South Head, 33°44'S, 151°34'E, May 1924, 137–146 m, C. W. Mulvey on S.S. *Goonambee* (AM P9489, Baker's 1926 specimens). 2 mancas (4.0, 5.0 mm), E of Port Jackson, 33°50'S, 151°33'E, 18 Dec 1985, 135 m, J. K. Lowry, R. T. Springthorpe and P. Colman, FRV *Kapala* (AM P41852). 3♀ (ovig. 8.0 mm, non-ovig. 5.0, 5.7), 4 mancas (3.7, 4.5, 4.7, 5.4 mm), off Nowra, 34°59.52'S, 151°5.95'E, 14 July 1986, 204 m, coarse shell, G. C. B. Poore et al. (NMV J31526, J19158). Manca (3.6 mm), dredged, 132–141 m, FRV *Kapala* (AM P41310). ♀ (non-ovig. 7.0 mm) (AM P41316).

Victoria. 3♂ (6.7, 7.2, 7.4 mm), 4♀ (non-ovig. 6.0, 6.0, 6.3, 7.7 mm), 9 mancas (3.0–6.0 mm), 38 km SW of Cape Paterson, 38°55.5'S, 145°17.0'E, 12 Nov 1981, 70 m, fine sand, R. Wilson (NMV J26296, J26412).

Tasmania. ♀ (non-ovig. 6.0 mm), 15 km E of Maria I., 42°37'S, 148°20'E, 9 Oct 1984, 102 m, R. S. Wilson (NMV J31528). 3 mancas (3.4, 3.7, 4.3 mm), off SE Maria I., 42°37.00'S, 148°12.50'E, 23 Apr 1985, 100 m, fine muddy bryozoa, R. S. Wilson (NMV J31527). ♂ (7.1 mm), 2 mancas (3.5, 4.0 mm), 15 km E of Cape Conella, 43°24.6'S, 147°32.5'E, 22 Oct 1984, 82 m, R. Wilson (NMV J26363).

Description of male. Body smooth, covered with clear gel-like layer; about 1.6 times as long as wide, widest at pereonite 4. Pereonite 1 longer than 2, 2–6 subequal in length; pereonite 7 less than half as long as pereonite 6, lateral margins not extending to full width of pereonite 6. Pleon with prominent large rounded dorsal boss. Pleotelson anterolateral angles forming acute points, posterior margin with points acute.

Antennule peduncle articles not flattened, article 1 longer (1.2) than combined lengths of articles 2–4; article 2 1.6 times as long as article 3; article 4 0.35 (35%) length of article 4; flagellum shorter (0.8) than peduncle, with about 14 articles. Antenna peduncle article 1 short, articles 2–4 subequal in length with 3 shorter than either 2 or 4, article 5 longest, longer than combined lengths of articles 3 and 4; flagellum slightly longer than peduncle, with 13 articles.

Mandible palp with 10 biserrate spines on distolateral margin, distal 2 of which are longest, article 3 with 9 biserrate spines. Maxilla lateral and middle lobes each with 5 setae, mesial lobe with about 10 prominent pectinate and plumose spines. Maxilliped palp articles 2–5 with about 8, 12, 12 and 10 setae respectively on mesial margin; endite distal margin with 9 plumose and 1 simple spine.

Pereopod 1 robust, posterior margins without setulose fringe ischium anterior margin with small proximal and larger distal acute spine; merus with 2 acute spines at anterodistal angle, 4 robust acute spines on posterior margin; carpus with 2 robust acute spines on posterior margin; propodus with 3 robust acute spines on posterior margin; dactylus about 0.6 length of propodus, with acute prominent accessory spine; posterior margins of merus to dactylus with scales. Pereopods 2–7 slender, with setulose fringe and scales on posterior margins.

Penes apically narrowed, about 3 times as long as basal width.

Pleopod 1 exopod and endopod with about 30 and 20 PMS respectively. Pleopod 2 and exopod and endopod with about 31 and 20 PMS respectively; appendix masculina 8 times as long as greatest width, 1.2 as long as endopod. Pleopod 3 exopod and endopod with about 30 and 18 PMS respectively. Pleopod 4 with simple marginal setae on proximal lateral margin of exopod and 2 simple setae on distal extremity; endopod with one simple setae. Pleopod 5 with simple marginal setae on proximal lateral margin distal lateral margin with setule fringe. Uropod with both rami acute, endopod 3 times as long as wide; exopod about 0.45 length of exopod.

Female. A single ovigerous female was present in the material examined, but lacked ova. Mouthparts metamorphosed; marsupium formed from oostegites arising from coxae of pereopods 1–4, overlapping at midline.

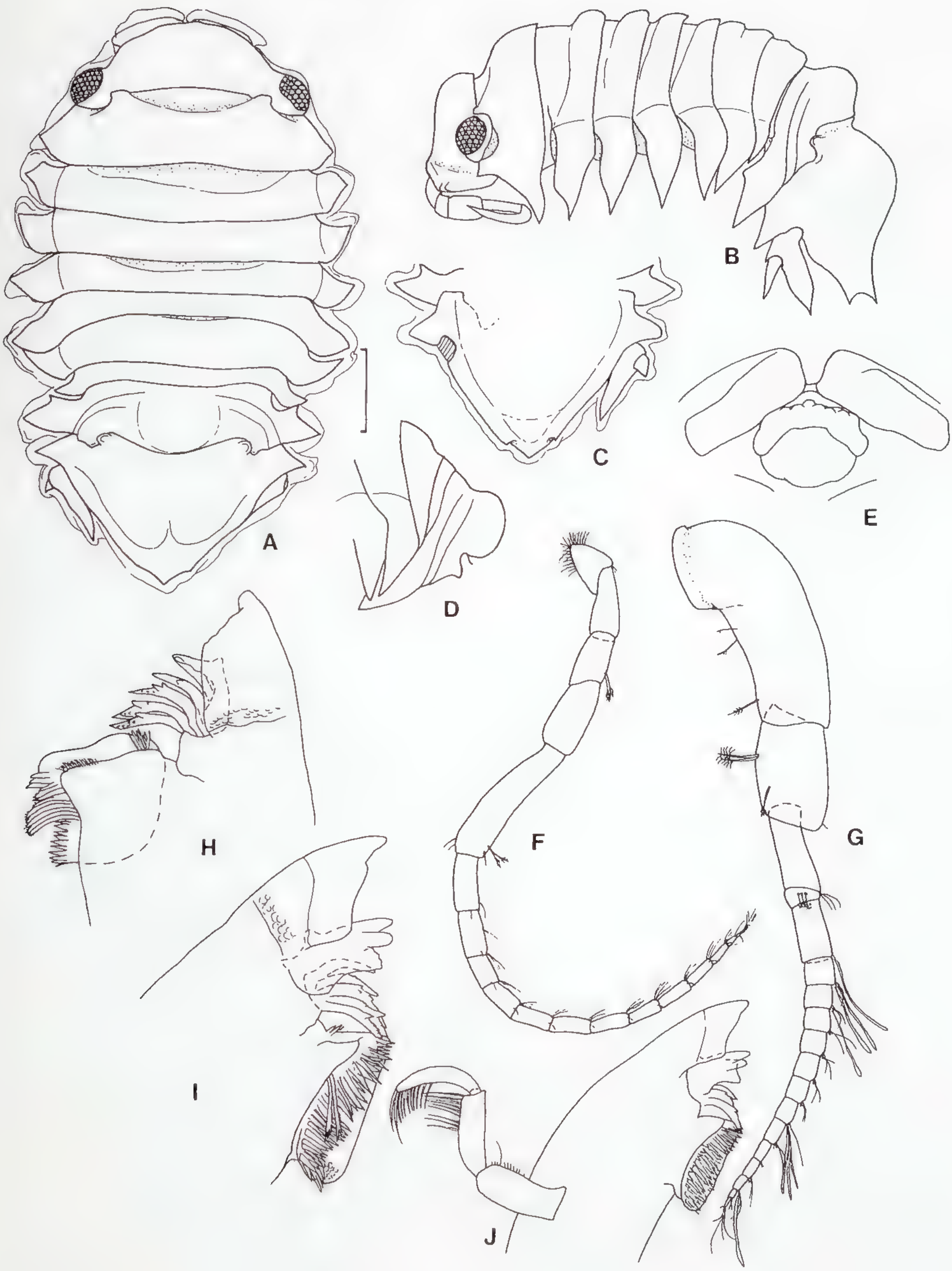

Figure 7. *Cassidinella incisa*. All figs ♂ 7.1 mm (NMV J26363). A, dorsal view (showing gel-jacket); B, lateral view; C, pleotelson, ventral view; D, pleon, showing segmentation; E, frons; F, antennule, G, antenna; H right mandible, distal portion; I, left mandible, distal portion; J, mandible. Scale line 1.0 mm.

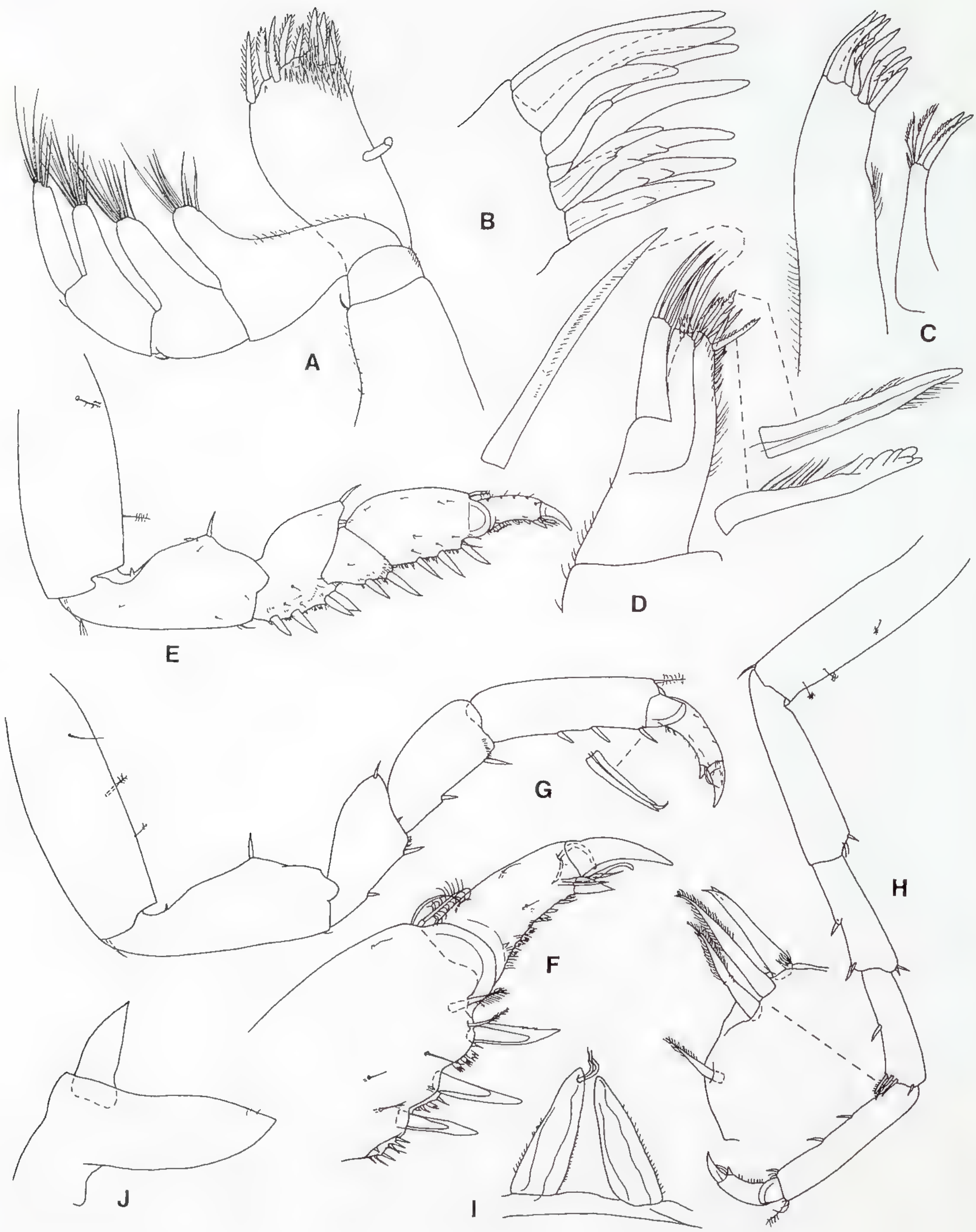

Figure 8. *Cassidinella incisa*. All figs ♂ 7.1 mm (NMV J26363). A, maxilliped; B, maxillule lateral lobe detail; C, maxillule; D, maxilla; E, pereopod 1; F, pereopod 1 distal propodus and dactylus; G, pereopod 2; H, pereopod 7; I, penes; J, uropod.

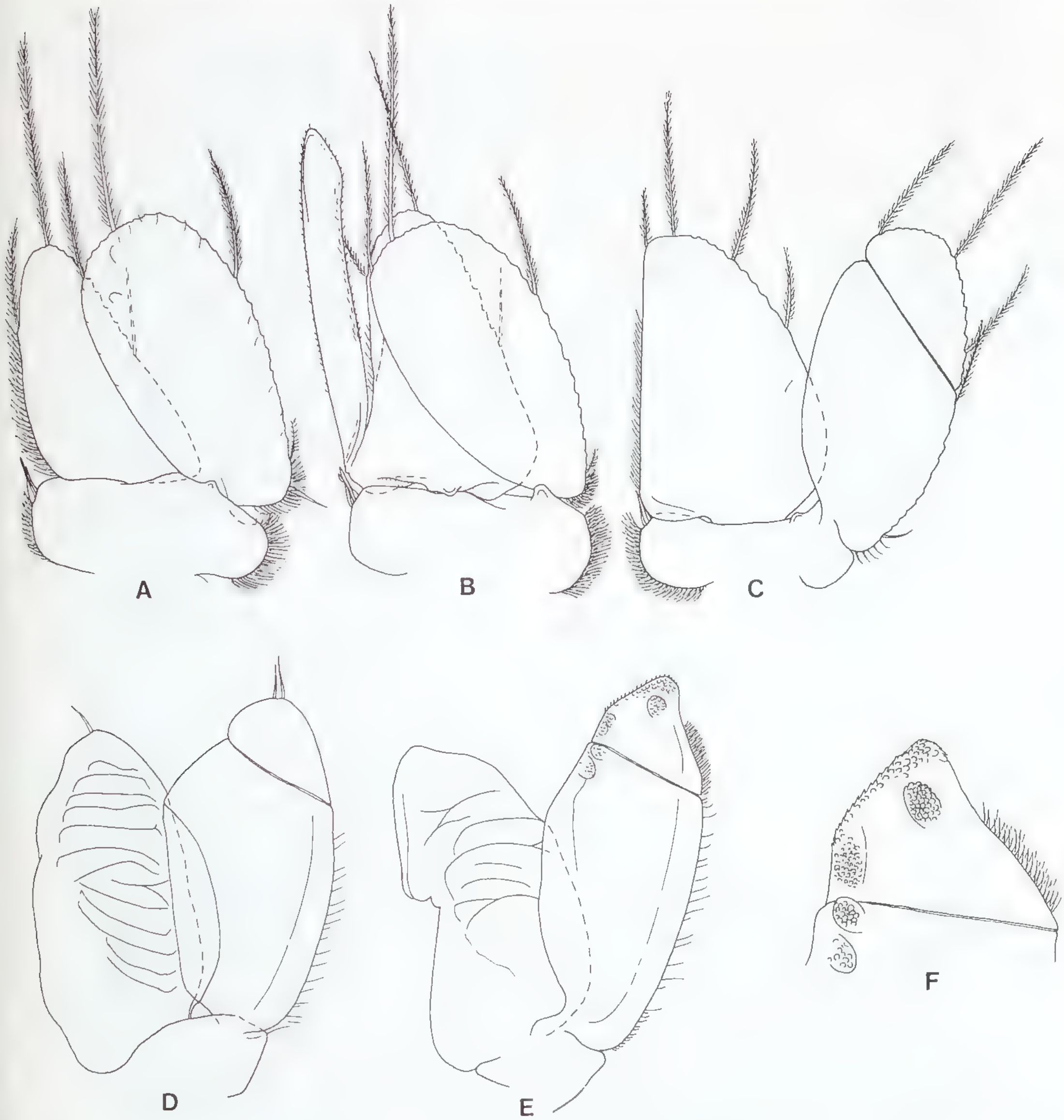

Figure 9. *Cassidinella incisa*. All figs ♂ 7.1 mm (NMV J26363). A–E, pleopods 1–5 respectively; F, detail, pleopod 5 exopod, distal margin.

Colour. Pale cream in alcohol; pereopods 1–6 and pleopods with few black chromatophores.

Size. Males 6.0–7.4 mm, non-ovigerous female 5.0–8.5 mm, mancas 3.0–6.0 mm.

Distribution. South-eastern Australia from in the vicinity of Sydney, NSW, eastern Victoria and south-eastern Tasmania at depths between 74 and 204 metres; the holotype was recorded from a depth of 43–66 fathoms (78–121 m) (Whitelegge, 1901), but Australian Museum data indicates 20–27 m. Substratum records are fine sand, and coarse shell.

Remarks. Readily recognized by the smooth unornamented cuticle, unflattened antennule articles 1 and 2, narrowed pereonite 7, and pereopod 1 with a total of 9 prominent acute spines on posterior margin of merus, carpus and propodus.

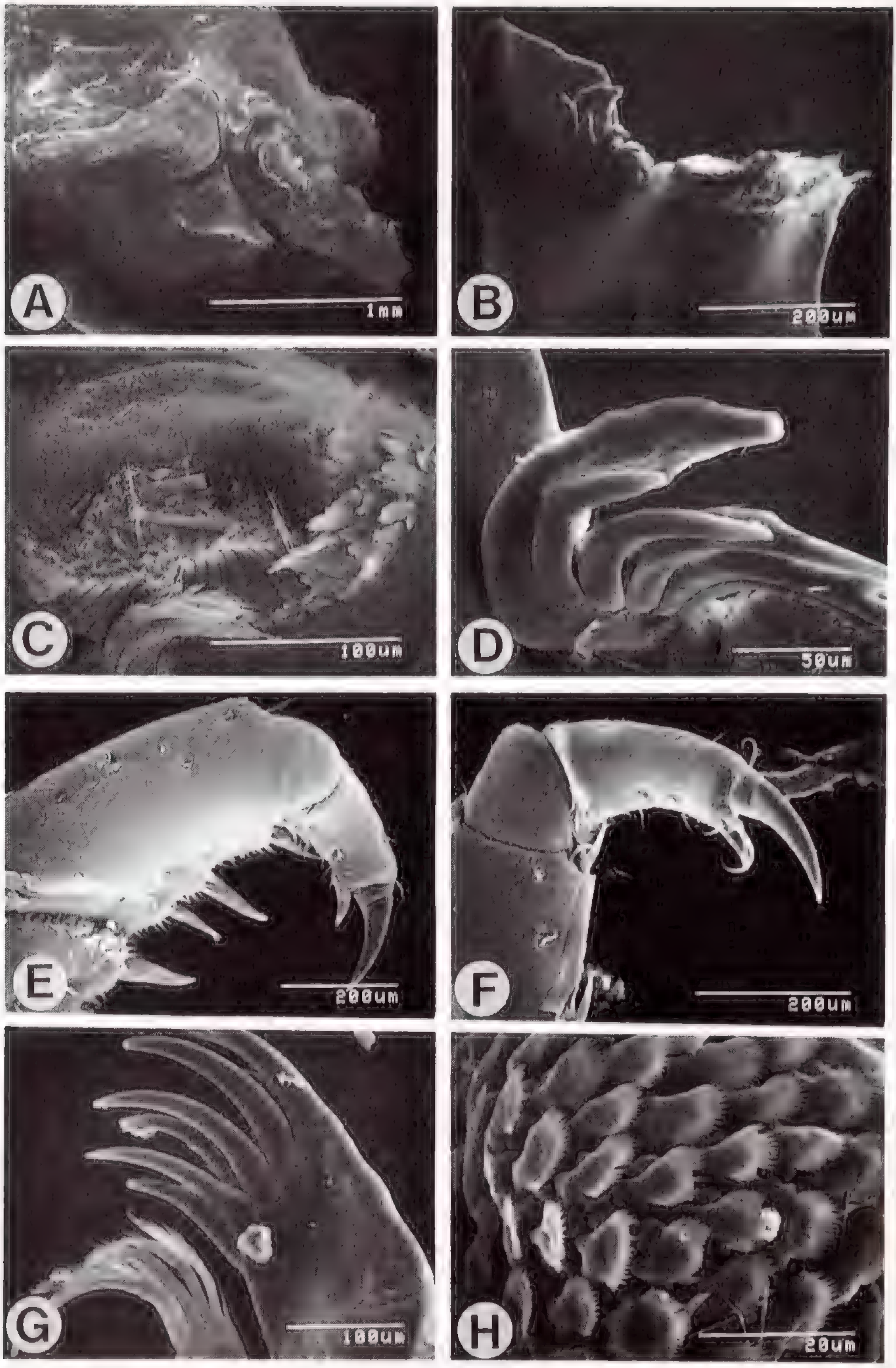

Figure 10. *Cassidinella incisa*. ♂, NMV J26412. A, anterior view of head B, right mandible; C, molar, *en face*; D, spine row; E, pereopod 1, propodus, dactylus; F, pereopod 2, distal propodus and dactylus; G, maxillule; H, pleopod 5 scale patch.

The description is based primarily on specimens from off Cape Conella (NMV J26363).

Cassidinella akania sp. nov.

Figure 11

Material examined. Holotype. ♀ (non-ovig. 5.7 mm), 36 km SW of Stokey Point, King I., Tas., Bass Strait, 40°26.7'S, 143°41.4'E, 22 Nov 1981, 85 m, medium sand, R. Wilson (NMV J31529).

Paratype. ♂ (imm. 5.0 mm), 40 km SSW of Warrnambool, Vic., 38°42.8'S, 142°35.6'E, 20 Nov 1981, 69 m, coarse sand, R. Wilson (NMV J31530).

Additional material. ♂, manca, western Bass Strait, 55 km SW of Cape Otway, Vic., 39°16.7'S, 143°06'E, 21 Nov 1981, 95 m, medium sand, R. Wilson (NMV J34872).

Description of male (imm.). Body with abundant setae and spines, about 1.4 times as long as wide, widest at pereonite 6; gel-like layer present but not obvious. Pereonite 1 longer than 2, 2–7 subequal in length; pereonite 7 as wide as pereonite 6.

Cephalon with 2 prominent conical submedial bosses; pereonite 1 with 2 prominent submedian bosses. Pleon with single median boss. Pleotelson with 2 prominent bosses, posterior margin flat, with 3 rounded points.

Antennule peduncle articles 1 and 2 strongly flattened prominently visible in dorsal view, article 2 anteriorly slightly longer than 1, anterolateral margin produced; articles 1 and 7. with abundant acute spines over surface; peduncle article 3 about 0.3 as long as article 2; flagellum short, about 0.3 as long as peduncle, with 6 articles. Antenna with article 5 longest; flagellum shorter than peduncle, with 8 articles.

Pereopod 1 with anterodistal spines of ischium and merus pectinate; posterior margins of merus, carpus and propodus with 2, 1 and 2 biserrate spines respectively; dactylus 0.66 length of propodus, accessory unguis prominent, slender, about 4 times as long as basal width; posterior margin of propodus with prominent serrate scales. Pereopods 2–7 subsimilar, pereopod 7 with longer biserrate spines on carpus than pereopod 2.

Uropod with abundant acute spines; peduncle anterolateral margin produced to form acute lobe, about 0.4 times as long as wide; exopod 0.6 as long as endopod; apices of both rami acute.

Female. Similar to the male, but ovigerous females (and adult males) not known.

Colour. Pale tan to cream in alcohol.

Distribution. Western Bass Strait, off southern end of King I., and off Warrnambool, 69–95 metres.

Etymology. The epithet is derived from the Greek *akanos*, a kind of thistle (i.e. prickly).

Remarks. Although no fully adult male is present, this distinctive species is still easily recognized. The genus does not exhibit strong sexual dimorphism, and body ornamentation (as evidenced by mancas, females, immature males and males of *E. incisa*) is unlikely to alter substantially on maturity. Given the scarcity of specimens of this species in the large collections of both the Australian Museum and the Museum of Victoria, the decision has been made to describe *Cassidinella akania* using the existing material.

The species can readily be identified and discriminated from its only congener by the prominent conical bosses on the cephalon, pereonite 1, pleon and pleotelson, by the flattened antennule peduncle, and by the densely setose and spinose body surfaces. The description was prepared from the dissected male paratype and female holotype. The holotype was not dissected in order to avoid damaging the specimen.

The immature male has paired submedian penes on sternite 7 but lacks an appendix masculina. The non-type specimens differ from the types only in having a more cospicuous and intact gel-like layer and so appearing less setose.

Dynameninae Bowman

Exocerceis Baker

Exocerceis Baker, 1926: 271. — Harrison, 1984: 380. — Harrison and Ellis, 1991: 939.

Exocirceis — Nierstrasz, 1931: 217 (lapsus).

Type species. Cerceis nasuta Whitelegge, 1902, subsequent designation by Baker (1926).

Diagnosis of male. Body vaulted, dorsal surface coarsely pitted. Cephalon anterior margin produced, concealing antennule bases in dorsal view; prominent posteriorly directed rostral process in ventral position; eyes with facets distinct pereonite 1 longest, pereonites 2–6 subequal in length, 7 longer than 2–6, slightly shorter than 1; coxae ventrally narrowed, posterior margin overlapping anterior margin of next coxa. Pleon with 4 segments, segment 1 entire, 2 separate sutures, anterior running to lateral margin, posterior to posterolateral margin. Pleotelson with apical notch between 2 acute points, third dorsal median point projecting over notch. Pereonite 1 without sternite; pleon with long sternal

Figure 11. *Casidinella akania* sp. nov. Figs A–D, holotype, remainder ♂ paratype. A, dorsal view; B, lateral view; C, frons; D, pleotelson, ventral view; E, antennule; F, antenna; G, maxillule, lateral lobe; H, maxilliped endite; I, pereopod 1; J, pereopod 1, distal propodus and dactylus; K, pereopod 2; L, pereopod 7; M, pleopod 1; N, pleopod 2; O, spines from distal margin of carpus, pereopod 7. Scale line 1.0 mm.

extension and sternal process extending to pleopod bases.

Epistome not projecting between antennule bases, not anteriorly produced. Antennule peduncle articles 1 and 2 robust, calcified, article 3 slender, flagellum shorter than peduncle. Antenna peduncle slender, articles 1–3 short, 5 longest; flagellum shorter than peduncle. Mandible incisor prominently tridendate, prominent tridentate lacinia mobilis present on left mandible, spine row with 5 (left) or 7 (right) pectinate spines; molar process prominent with abundant marginal teeth, gnathal surface weakly nodulose. Maxilla mesial lobe with 4 large serrate spines, and 2 small spines; lateral lobe with 10 spines, some of which are serrate. Maxilla entire, setae on lateral and middle lobes very finely serrate. Maxilliped palp articles 2–4 mesial margin forming finger-like lobes; endite distal margin subtruncate with slender circumplumose setae, single smooth spine at distomesial angle.

Pereopods all robust, ambulatory, dactylus with short acute accessory spine; articles generally without long setae, or prominent spines; pereopod 1 shorter and stouter than pereopods 2–7 which are subsimilar.

Penes short, set well apart, not reaching pleonal sternite.

Pleopods 1–3 with PMS on both rami, 4 and 5 without PMS. Pleopod 1 endopod triangular, exopod with truncate distal margin; both rami with longitudinal axes oblique to peduncle; peduncular coupling hooks short and stout. Pleopod 2 rami similar to pleopod 1, but exopod distolateral margin with toothed, distal margin with prominent plumose spines; endopod with appendix masculina in medial position. Pleopod 3 endopod collinear with peduncle; exopod oblique, without transverse suture. Pleopod 4 exopod with small scaled patch on mesial margin, both rami with distinct clearly defined ridges. Pleopod 5 exopod with simple setae on lateral margin, 3 scale lobes distally; both rami with distinct clearly defined ridges. Uropod rami distal margins deeply serrate, not acute or produced, extending slightly beyond pleotelson apex.

Female. Ovigerous females not present in the material examined. Non-ovigerous females differ from males in lacking three acute points on the posterior of the pleotelson, having instead an apically produced, ventrally open notch.

Remarks. The principal differential characters recognized by Baker (1926) and used in the key of Harrison and Ellis (1991) were the produced unflattened anterior margin to the cephalon, article 1 of the antennule peduncle without an acute process (i.e. distal margin blunt) and the bluntly rounded distal margin of the uropodal exopod (not truncate as stated by Harrison and Ellis, 1991). To these, the following characters can be added: pleopod 1 rami without serrate margins, pleopod 2 exopod distal margin with about 8 prominent spines (rather than the usual PMS), pleopod 3 exopod without transverse suture; uropodal rami with deeply serrate distal margins.

The genus is monotypic.

Exocerceis nasuta (Whitelegge)

Figures 12–15

Cerceis nasuta Whitelegge, 1902: 276, figs 36a–b.
Exocerceis nasuta - Baker, 1926: 272, pl. 48 figs.10–12.
Exocirceis nasuta - Nierstrasz, 1931: 217 (lapsus?).

Material examined. Syntypes. 4♀ (non-ovig. 4.7, 5.8 mm, 1 dissected, 1 without head), 6 km E of Wattamola, NSW, 34°10'S, 151°11'E, 22 Mar 1898, 99–108 m, mud, E. R. Waite on H.M.C.S. *Thetis* (AM G2279). ♂ (poor condition, + appendages), 2 km E of Crookhaven R., NSW, 34°14'S, 150°48'E, 20–27 m, sand and rock, E. R. Waite on H.M.C.S. *Thetis* (AM G2277).

Other material. Queensland. 1 (crushed), off Moreton I., 27°27'S, 153°39'E, 29, Mar 1969, 77 m (AM P41857).

New South Wales: ♂ (5.6 mm), 6 mancas (1.5–1.7 mm, post partum), off Newcastle, 32°53'S, 152°35'E, 15 Aug 1985, 175 m, FRV *Kapala* (AM P41859). 2♀ (non-ovig. 3.4, 5.0 mm), E of Long Reef, 33°43'S, 151°46'E, 14 Dec 1985, 174 m, J. K. Lowry and R. T. Springthorpe on FRV *Kapala* (AM P41277). 2♂ (5.6 dissected, 6.0 mm), 22♀ (non-ovig. 3.4–5.2 mm, mean = 4.3 mm; 25 unmeasured), E of Long Reef, 33°43'S, 151°46'E, 20 Dec 1985, 174 m, J.K. Lowry et al., on FRV *Kapala* (AM P41856, P41858). ♀ (non-ovig. 5.2 mm), off Nowra, 34°59.52'S, 151°05.94'E, 14 Jul 1986, 204 m, coarse shell, G. C. B. Poore et al. (NMV J19154).

Description of male. Body about 2.3 times as long as wide; widest at pereonite 6. Pleon with 4 or 5 sublateral granular longitudinal ridges. Pleotelson with 2 large bilaterally compressed bosses.

Antennule peduncle article 1 longest, 2.3 times as long as article 2, 1.8 times as long as article 3; flagellum with 6 articles, extending to posterior of pereonite 1. Antenna peduncle article 4 1.8 times as long as 3, article 5 1.3 times as long as 4; flagellum shorter than peduncle, with 10 articles, extending to pereonite 2. Mandible palp article 2 with about 4 serrate setae on distolateral margin, article 3 with 10 serrate setae on distolateral margin. Maxilla with 7 and 8 setae on lateral and middle lobes; mesial lobe with 2 prominent and about 8 smaller stout plumose spines setae. Maxilliped endite distal margin with 3 sub-

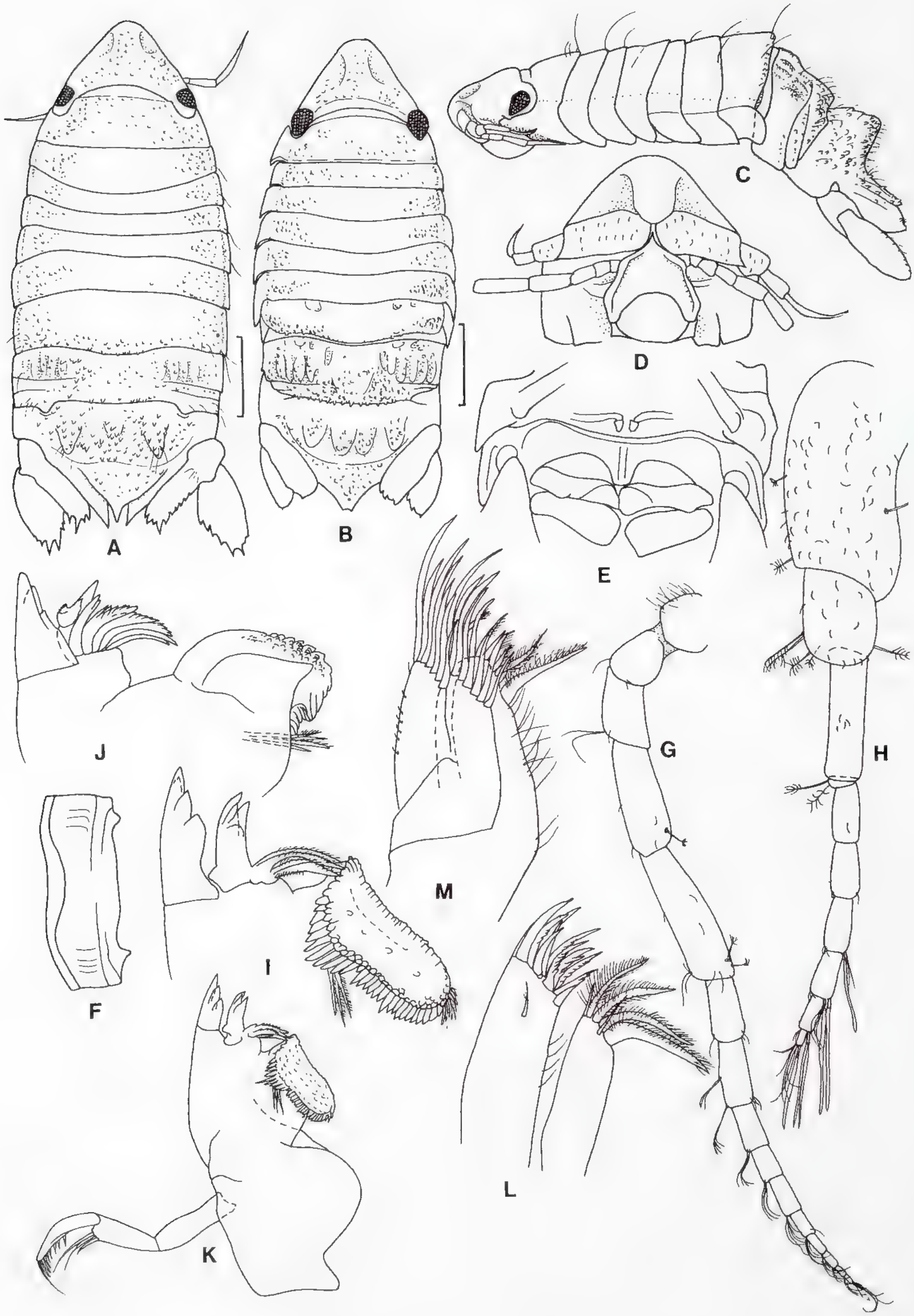

Figure 12. *Exocerceis nasuta*. A, C–F, male 6.0 mm. G–L, male 5.6 mm (AMP41858), unless otherwise indicated. A, dorsal view; B, 5.8 mm♀ syntype (AM G2279); C, lateral view; D, frons; E, pleonal sternite and penes; F, pleonal sutures; G, antennule; H, antenna; I, left mandible, distal portion; J, right mandible; K, mandible; L, maxillule; M, maxilla. Scale lines 1.0 mm.

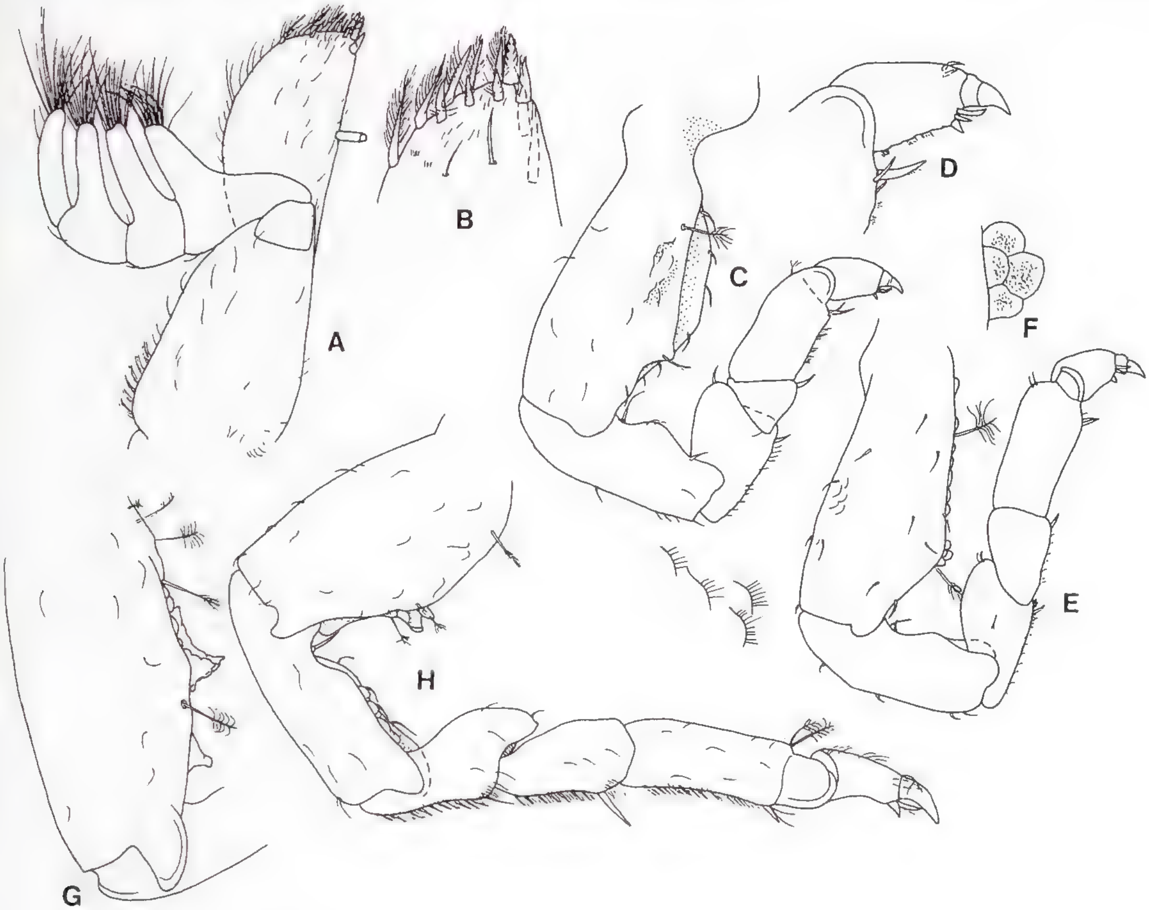

Figure 13. *Exocerceis nasuta*. All figs, male 5.6mm (AMP41858). A, maxilliped; B, maxilliped endite, detail; C, pereopod 1; D, pereopod 1, dactylus; E, pereopod 2 (plus detail of cuticular scales); F, pereopod 2, cuticular scale, anterior margin of basis, G, pereopod 6, basis; H, pereopod 7.

marginal plumose spines, 4 acute marginal spines and 1 simple and one cactus spine; dorsal distomesial margin with 2 densely plumose spines; endite with about 12–14 setae each on lobes of articles 2–5.

Pereopod 1 robust, propodus and merus subequal in length, carpus short, triangular; dactylus about 0.6 as long as propodus, unguis short, about 0.3 as long as dactylus; accessory unguis small, acute; basis anterior margin with cuticular process; posterior margin with single acute spine at posterodistal angle of merus, carpus and propodus. Pereopod 2 similar to 1 but more slender; posterior margin of basis with epicuticular nodule on anterior margin. Pereopod 3 merus to carpus more elongate than in pereopods 1 and 2; posterior margin of merus, carpus and ischium with scales and setules; pereopods 4 to 7 generally similar to 3, becoming progressively longer.

Penes short, set wide apart, distally rounded. Pleopod exopod with about 26 PMS, endopod with 11.

Pleopod 2 appendix masculina slightly shorter (0.94) than length of endopod mesial margin, inserted about 0.36 along length of mesial margin, straight apex bluntly rounded; exopod with 15 PMS and distally 6 stout plumose spines; distolateral angle with 2 prominent serrations, endopod with 20 PMS. Pleopod 3 exopod with about 32 PMS, endopod with 14. Uropod with prominent simple spines on endopod surface, lateral surface of peduncle and lateral margin of exopod; lateral margin of endopod and mesial margin of exopod with short PMS; both rami with deeply bifid apices.

Female. Similar to male except dorsal surface of pleotelson appears to have 4 indistinct longitudinal ridges and posterior margin formed into

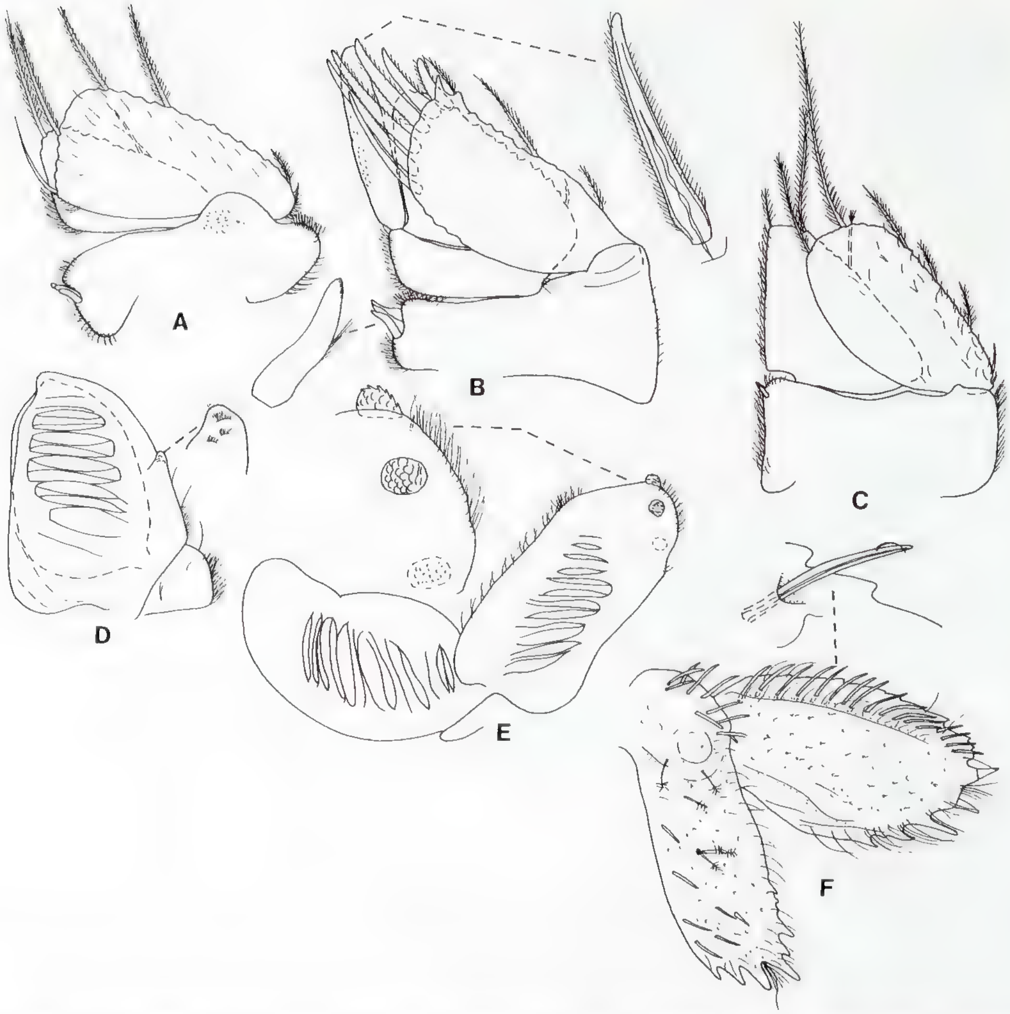

Figure 14. *Exocerceis nasuta*. All figs, male 5.6 mm (AMP41858). A–E, pleopods 1–5 respectively; F, uropod.

ventrally open, posteriorly directed tube, lacking the three acute lobes of male. Ovigerous females not present in material examined.

Colour. Pale cream in alcohol.

Size. Males 5.6–6.0 mm, non-ovigerous females 3.4–5.8 mm.

Distribution. Off Moreton I., south-eastern Queensland (one record) to central NSW coast between Nowra and Newcastle, at depths between 20 and 204 metres.

Remarks. While superficially similar to some *Cerceis* species, the blunt anterior margin of the cephalon and uropod exopod being bluntly rounded immediately identifies both the genus and the species, as does the presence of prominent plumose spines on the pleopod 2 endopod.

The description is based primarily on specimens from off Long Reef (AM P41858).

Acknowledgments

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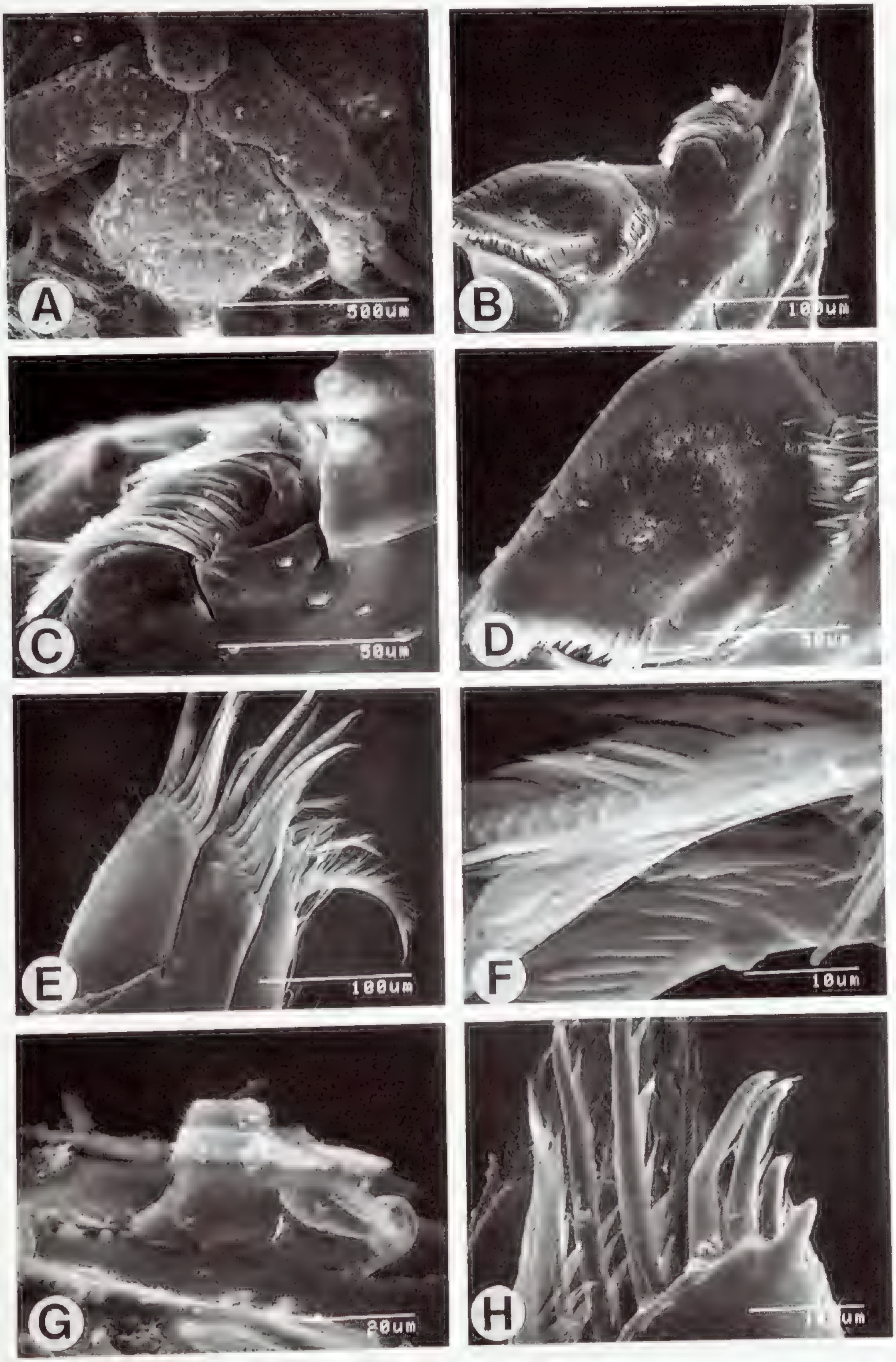

Figure 15. *Exocerceis nasuta*. ♀ (AM P41858). A, frons; B, left mandible, distal portion; C, spine row, left mandible; D, molar, *en face*; E, maxilla; F, spines, maxillule, mesial lobe; G, cuticular scales, pereopod 7; H, pleopod 2, exopod spines.

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Memoirs of the Museum of Victoria 54: 171–178 (1994)

MARICOCCUS BRUCEI, AN UNUSUAL NEW GENUS AND SPECIES OF SPHAEROMATIDAE FROM SOUTHERN AUSTRALIA (CRUSTACEA: ISOPODA)

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Abstract

Poore, G. C. B., 1994. *Maricoccus brucei*, an unusual new genus and species of Sphaeromatidae from southern Australia (Crustacea: Isopoda). *Memoirs of the Museum of Victoria* 54: 171–178.

A new monotypic genus is diagnosed, the first among Sphaeromatidae with complete fusion of pleonite 1 to the remaining pleonites. It belongs to a group of dynamenine genera in which the first pleopods are operculiform, the first pleonal sternite is long, and the mandibular incisor is unicuspidate. The new genus is exceptionally flattened, more than in species of *Juletta* Bruce, 1993 and *Margueritta* Bruce, 1993 which it resembles. It differs from these two in the possession of falcate pereopodal dactyli.

Introduction

The sphaeromatid subfamily Dynameninae Bowman is characterised principally by the presence of thickened folds on both rami of pleopods 4 and 5. With about 35 genera it is the largest subfamily of the Sphaeromatidae. Six of its genera are associated in what seems a monophyletic clade united by the possession of operculate or semioperculate pleopods 1, pleopod 2 with endopod very much longer than exopod, and a complete sternite on pleonite 1. The six are: *Ischyromene* Racovitza (Harrison and Holdich, 1982); *Amphoroidea* Milne Edwards (Baker, 1908); *Amphoroidella* Baker (Harrison, 1984); *Cymodocella* Pfeffer (Brandt and Wägele, 1989); *Juletta* Bruce; and *Margueritta* Bruce (Bruce, 1993). Other undescribed genera are known (N. L. Bruce, pers. comm.) and other species may be assigned to the group when their pleopods have been described. The monophyly of the clade is as yet untested.

A new similar genus and species from southern Australia, *Maricoccus brucei*, is here described.

Material is lodged in the Australian Museum, Sydney (AM), Queensland Museum, Brisbane (QM), Museum of Victoria, Melbourne (NMV), and South Australian Museum, Adelaide (SAM).

Maricoccus gen. nov.

Type species. *Maricoccus brucei* sp. nov.

Diagnosis. Body strongly flattened, smooth; pereonites 6 and 7 without dorsal processes. Head strongly flattened, anteriorly produced, with ventral rostrum between antennae; eyes small, lateral, visible in both dorsal and ventral views. Coxae 2–7 fused to tergite, laterally expanded, interconnected by coxal keys, visible ventrally; coxa 7 reaching to lateral margin of body. Pleonite 1 completely fused to remaining pleonites, indicated mid-laterally by short slit; all pleonites fused to pleotelson, 1 suture probably between pleonites 5 and 6; pleotelsonic apex entire, without foramen or exit channel. Pleonite 1 sternite long, with plate between pleopods 1.

Epistome (fused frontal lamina and clypeus) broad, not extending between antennae 1. Antenna 1 peduncle not flattened, article 2 produced distally. Mandibular incisor unicuspidate; lacinia mobilis absent; spine row of prominent slender truncate spines; molar process blunt, not ornamented. Maxilla 2 outer lobe short, with 1 seta. Maxillipedal endite with clubbed setae mesially; palp articles 2–5 without lateral setae, with mesial setae; articles 3 and 4 weakly lobed.

Pereopod 1 shorter than 2–7, each with falcate dactylus about as long as propodus. Penes paired on posterior margin of pereonite 7, not reaching pleopods 1.

Pleopods 1 and 2 together operculiform; pleopod 1 short, exopod weakly indurate; pleopod 2 endopod weakly indurate, much longer than exopod, concealing remaining pleopods. Pleopod 3 exopod without transverse suture. Pleopods 4 and 5 with thickened ridges on both rami; exopods without suture; pleopod 5 exopod with 2 scaled lobes. Pleopods 1–3 only with plumose marginal setae. Uropods lamellar, meeting in midline posteriorly, rami not reduced.

Female. Mouthparts not metamorphosed. Oostegites present on pereopods 2–4, overlapping in midline. Body and appendages as in male.

Etymology. From the Latin *mare* (the sea) and *Coccus* (a Linnean genus of scale insect) alluding to the origin and shape of the type species (masculine).

Remarks. Maricoccus is the first-recorded sphaeromatid with complete fusion of pleonite 1 to the remaining pleonites and telson. The usual sphaeromatid condition is a three-part pleon: very short free pleonite 1 whose epimera do not reach the lateral margin of the body; fused pleonites 2–5 with epimera variously indicated laterally: and pleotelson (pleonite 6 plus telson). In *Maricoccus* there is no indication of pleonite 1 dorsally or laterally and the remaining pleotelsonic unit bears only one lateral suture, possibly indicating the suture between pleonites 5 and 6.

The features shared by *Maricoccus* and the dynamenine *Ischyromene*-group of genera are exposed and thickened proximomesial triangle of pleopod 1 endopod, endopod of pleopod 2 much longer than exopod, and the complete sternite of pleonite 1 with a medial posterior process. Individually, these characters may be seen in some other sphaeromatid genera but investigation of their distribution is beyond the scope of this contribution.

Pleopod 1 is very short in *Maricoccus* and is operculiform only in combination with pleopod 2, a situation very different from other genera of the group. Within the *Ischyromene*-group, *Maricoccus* is most similar to two genera also confined to southern Australia, *Juletta* and *Margueritta*. Both are flattened (weakly so in *Margueritta*), smooth, possess a ventral rostrum, and have a simple mandibular incisor. They also lack a complete suture between pleonites 5 and 6, a condition found rarely in Sphaeromatidae. The new genus differs from these two in being exceptionally flattened, in possession of falcate pereopodal dactyli, and simplicity of the molar process.

No adult male characters are used in this diagnosis since only one apparently mature male is available in the type species. This specimen, with well developed penes, lacks appendices masculinae. *Dynamene* Leach is the only sphaeromatid genus which has been shown convincingly to lack appendices masculinae (Holdich and Harrison, 1980) and the true generic condition is uncertain.

Maricoccus brucei sp. nov.

Figures 1–4

Material examined. Holotype. Vic., NW side of Henty Reef, Mounts Bay, Apollo Bay (38°47.0'S, 143°40.5'E), 3 May 1988, 18 m, red algae on boulder, R. T. Springthorpe and P. B. Berents, AM P41376 (♂, 4.6 mm, with 1 slide).

Paratypes. Victoria. Type collection, AM P41840 (non-ovigerous ♀, 3.3 mm; 6 mancas, 1.5–2.7 mm). Type locality but on bryozoan *?Orthoscuticella*, AM P41373 (manca, 2.3 mm). Laurence Rocks, Portland (38°24.0'S, 141°40.1'E), 30 Apr 1988, 23 m, on red algae, R. T. Springthorpe and P. B. Berents, AM P41345 (ovigerous ♀, 4.6 mm; 2 mancas, 1.6, 2.1 mm). 15 km S of Port Fairy (38°32.0'S, 142°28.6'E), 20 Nov 1981, 52 m, medium sand, R. Wilson (stn BSS-187), NMV J13266 (non-ovigerous ♀, 3.7 mm).

Tasmania. 14 km SW of Currie, King I. (40°00.7'S, 143°49.9'E), 46 m, fine sand, sled, R. Wilson (stn BSS-197), NMV J26276 (manca, 2.3 mm).

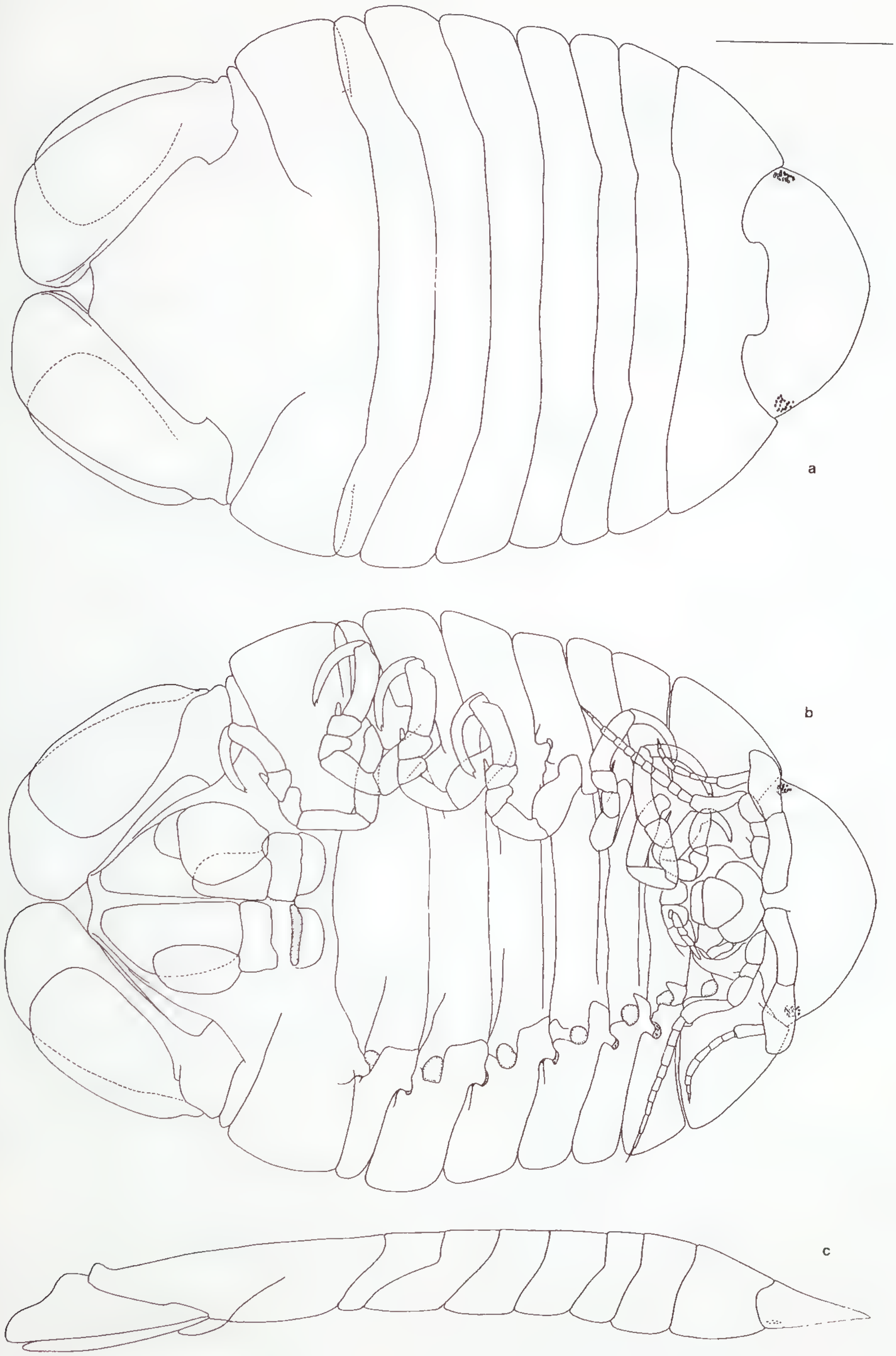
South Australia. E side of Wright I., Encounter Bay (35°35'S, 138°37'E), 10 May 1988, on bryozoan, 12 m, N. Holmes (QM W18928, non-ovigerous ♀, 3.4 mm). 0.8 km S of Henley Beach Jetty, Adelaide, 1.4 km offshore (34°45'S, 138°31'E), 1 Jan 1985, from *Amphibolis antarctica* community, 6–7 m, S. M. Clarke, SAM C5509 (juvenile, 4.4. mm, with 2 slides), SAM C5510 (2 juveniles, 3.1 mm), NMV J14028 (juvenile, 4.5 mm, with 1 slide). Beachport, Snapper Point (37°29.3'S, 139°59.6'E), 6 m, brown algae on limestone reef, G. C. B. Poore and R. S. Wilson, 14 May 1990, SCUBA (stn CRUST 90), NMV J20426 (juvenile, 2.6 mm).

Description. Male. Body 1.5 times as long (head to uropod) as wide, flat, 6 times as long as high, smooth. Head less than half width of body, anteriorly produced as a semi-circular plane, posterolaterally weakly inset into pereonite 1. Pereonite 1 longer and narrower than rest. Coxae extending about one-quarter of body width beyond bases of pereopods; adjacent coxal plates interconnected by ventral coxal keys. Pleonite 1 indicated only by short slit lateral to ventral key near base of pereopod 7. Pleotelson apex excavate, upturned, together with uropod endopods forming exit hole.

Eyes lateral, small. Epistome wider than long, curving around labrum; labrum weakly divided

→

Figure 1. *Maricoccus brucei*, juvenile, 4.4 mm, SAM C0000. a, dorsal view. b, ventral view (left pereopods and pleopod 1 removed). c, lateral view. Scale line = 1 mm.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b
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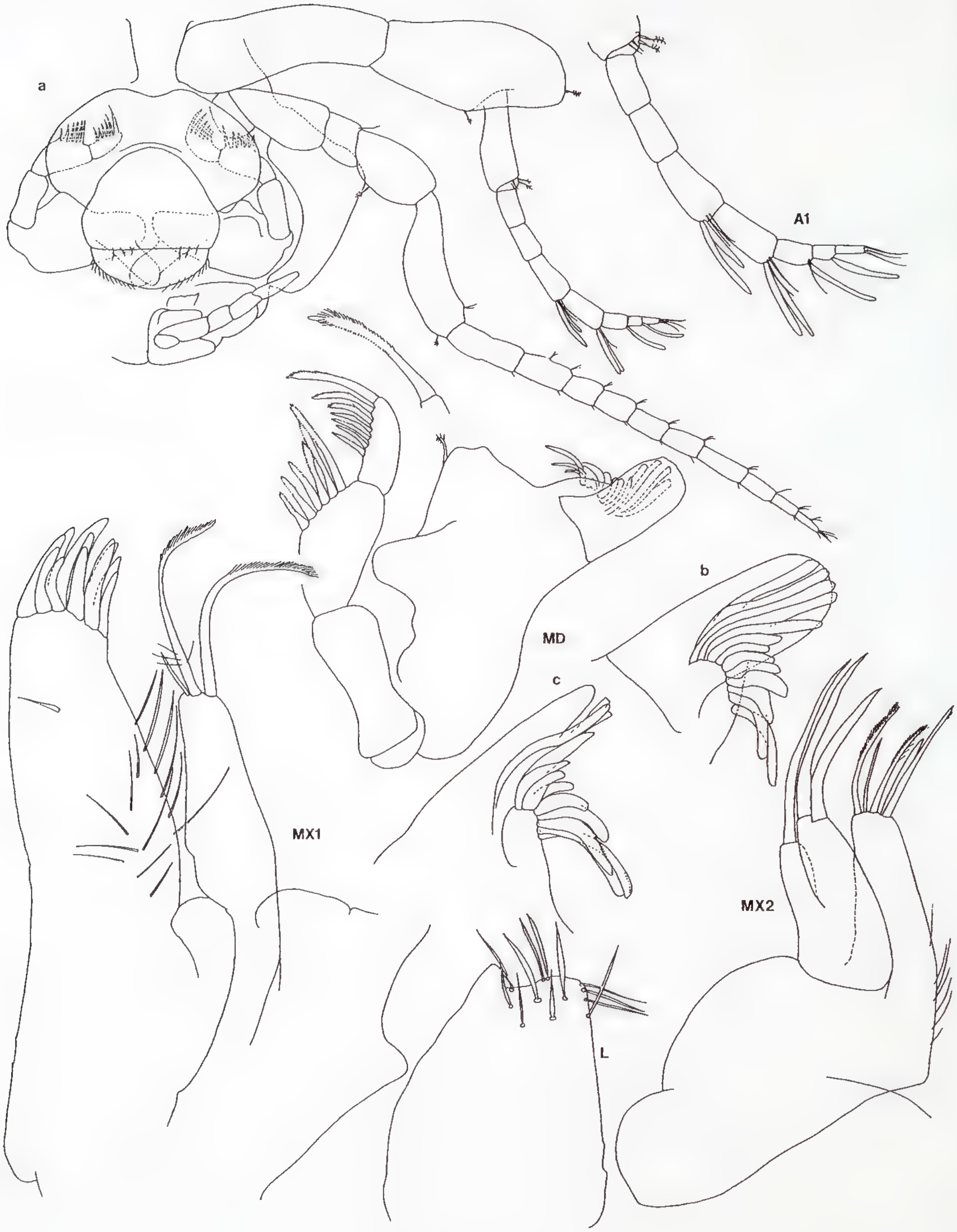

Figure 2. *Maricoccus brucei*, juvenile, 4.4 mm, SAM C5509. a, mouthparts and antennae in situ. A1, antenna 1. MD, mandible (a, right ventral; b, right incisor and spine row, anterior; c, left dorsal). MX1, MX2, maxillae 1, 2. L, left labium.

Figure 3. *Maricoccus brucei*, juvenile, 4.4 mm, SAM C5509. MP, maxilliped (a, right, posterior; b, right endite, posterior; c, left endite, anterior). P1, left pereopod 1 (a, lateral; b, propodus and dactylus, mesial; c, unguis, lateral). P2, left pereopod 2, lateral.

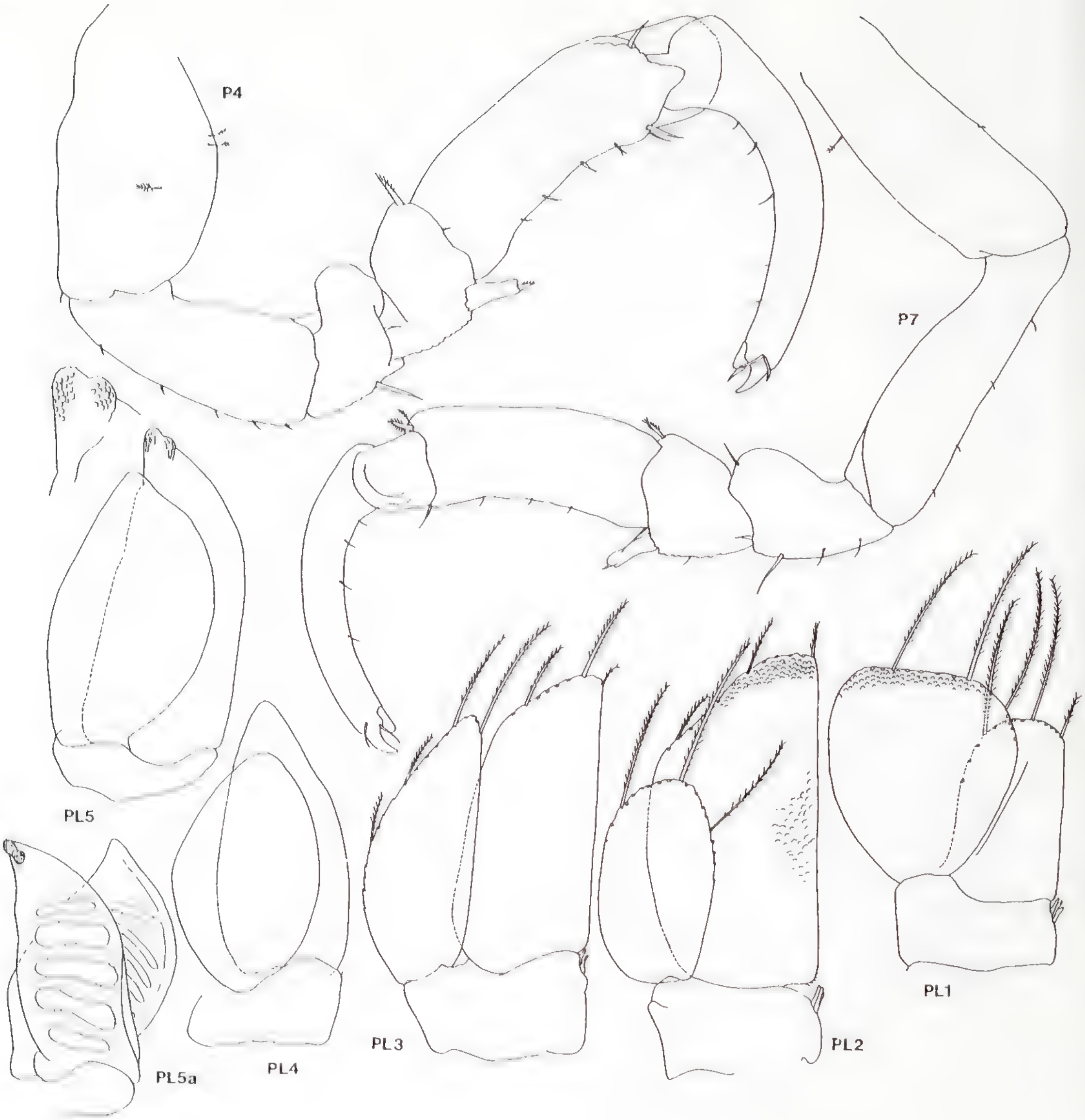

Figure 4. *Maricoccus brucei*, juvenile, 4.4mm, SAM C5509. P4, left pereopod 4, mesial. P7, left pereopod 7, lateral. PL1–PL3, left pleopods 1–3.

Juvenile, 4.5mm, NMV J14028. PL4, PL5, left pleopods 4, 5 (all pleopods to same relative scale, typical setae only shown).

Male, 4.6mm, AM P41376. PL5a, pleopod 5.

into proximal and distal parts, completely covering mandibular incisors.

Antenna 1 bases separated by ventral rostrum; peduncle article 2 0.8 length of article 1, anterodistally produced; article 3 articulating subterminally on 2, about half as long as article 2; flagellum shorter than peduncle, of 1 short and 7 longer articles bearing 0, 0, 2, 2, 1, 1, 0 aesthetascs. Antenna peduncle geniculate between articles 4 and 5; article 1 short; article 2 4 times as long as first; article 3 half as long as second; articles 4 and 5 progressively increasing in length; flagellum of 10 articles bearing minute setae.

Mandibles symmetrical; incisors chitinised, brown, oblique–posteriorly directed and overlapping, distally rounded; spine row of 12–13 flattened bent spines of which the longest lie against the incisor; molar process blunt, with basal seta; palp basal article held in over labrum; articles 1 and 2 subequal; 2 with 6 pectinate setae on distal half; 3 with 7 pectinate setae. Maxilla 1 inner lobe with 2 long setulate setae and 1 simple short seta; outer lobe with 11 short strong setae. Maxilla 2 laterally expanded; inner lobe with 5 setae of various forms; middle lobe with 2 setae; outer lobe shorter than middle, with 1 setae. Maxilliped without defined coxa or epipod; endite truncate, with 2 complex clubbed setae on anterior face near mesial margin; with 3 strong plumose setae on distolateral margin; 4 narrow fan-shaped spines on posterior face; and 1 simple coupling hook mesially. Maxillipedal palp 2.5 times as long as endite, article 1 short; articles 2–4 mesially lobed and setose; article 5 longer than 4, distally setose.

Pereopod 1 half length of other pereopods; merus and carpus with posterodistal setae; propodus with 4 mesial pectinate setae, dactylus as long as propodus, with short unguis and blunt accessory unguis. Pereopods 2–7 essentially similar; third slightly shorter than second; fourth to sixth of similar size; seventh slightly more elongate. Pereopod 4 merus with fine posterodistal spine; carpus with stout flagellate posterodistal spine and plumose anterodistal seta; propodus slightly curved, dactylar lateral articulating plate indicated by fine transverse suture, with few short posterior and anterodistal setae; unguis minute, secondary unguis blunt.

Paired penes on the posterior margin of pereonite 7, longer than wide.

Pleopod 1 overlapping only half pleopod 2, endopod shorter than exopod, with 14 setae on distolateral margin; exopod widest distally, almost as broad as long, with 18 distal setae, with thickened rugose distal margin. Pleopod 2 endopod 1.5 times as long as exopod, with 13 disolateral setae on oblique margin, thickened and rugose on distal and midmesial margin; exopod ovate, with 19 marginal setae on distal half. Pleopod 3 rami narrow, acute; endopod longer, with 8 setae; exopod curved with 30 setae. Pleopod 4 endopod longer and more acute than exopod, both rami with c. 7 transverse thickened ridges. Pleopod 5 endopod longer than exopod, with 2 apical scaled lobes, both rami with c. 5 transverse-oblique thickened ridges. Uropod attached near lateral suture of pleotelson; rami meeting posterior to apex of telson, length 2.5 times greatest width; exopod shorter, ventral, apex rounded–truncate.

Female. No ova- or embryo-bearing females observed.

Colour. Deep violet when alive (V. N. Sergeev pers. comm.); dull white–yellow in alcohol, semi-transparent.

Size. Up to 4.6 mm, mancas ranging from 1.5 to 2.7 mm.

Distribution. Shallow coastal waters of South Australia, Victoria and Tasmania at depths between 12 and 52 m, from red algae, bryozoans and sea grasses.

Etymology. For Niel Bruce in recognition of his contribution to the taxonomy of Australian isopods.

Remarks. Most of the specimens, including that illustrated, are small and lack transverse ridges on pleopods 4 and 5. They are, however, quite clear on the largest specimen, a male (fig. 4: PL5a). This specimen has small paired penes on the posterior margin of pereonite 7 but has no appendices masculinae. It is uncertain whether or not this is a fully adult specimen.

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NEW SPECIES OF *LYNSEIA* AND TRANSFER OF THE GENUS TO LIMNORIIDAE (CRUSTACEA: ISOPODA)

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Abstract

Cookson, L. J. and Poore, G. C. B., 1994. New species of *Lynseia* and transfer of the genus to Limnoriidae (Crustacea: Isopoda). *Memoirs of the Museum of Victoria* 54: 179–189.

Two new species of *Lynseia* are described: *L. annae*, in southern and central Western Australia, was taken from burrows in leaves of seagrasses of the thin-leaved *Posidonia australis* group: *P. australis* and *P. sinuosa*; *L. dianae*, in southern Western Australia and western South Australia, from the thick-leaved *Posidonia ostenfeldii* group: *P. coriacea*, *P. ostenfeldii* and *P. robertsoniae*. The type species, *L. himantopoda*, is also recorded from Western Australia, in burrows in *Heterozostera tasmanica*. On the basis of variability in mandibles and uropods the diagnosis of the genus is widened. Similarity of the limbs of the new species to those of *Limnoria* require it to be transferred to Limnoriidae White. The family Lynseiidae Poore is thereby placed in synonymy with Limnoriidae. A key to genera is presented.

Introduction

The discovery of two species of isopods similar to *Lynseia himantopoda* Poore, 1987, only member of the family Lynseiidae Poore, 1987, prompted a re-examination of this family and its relationships to Limnoriidae White. In this contribution the family status of the Lynseiidae is shown to be unsustainable and its only genus is placed in the larger family. A key to genera is presented, replacing that of Cookson (1991) who reviewed the Limnoriidae in detail.

All species of limnoriids are borers of plant material: *Paralimnoria* in wood, *Limnoria* in wood, algae or seagrass and *Lynseia* in seagrasses. It is tempting to suggest that the three species of *Lynseia*, which are confined to southern Australia, arose there from a seagrass-eating, *Limnoria*-like ancestor. By elongation and other adaptations they became obligate seagrass borers. Two species of *Limnoria* are recorded from seagrass in southern Australia, *L. agrostisa* Cookson and *L. raruslima* Cookson.

The three species of *Lynseia* are host specific (Brearley and Walker, 1993). *Lynseia himantopoda* is confined to the narrow-leaved *Heterozostera tasmanica* and is distributed with this species across southern Australia. The two new species burrow in the broader leaves of species of *Posidonia*. *Posidonia australis* Hook. *f.* and *P. sinuosa* Cambridge and Kuo belong to the *Posidonia australis* species group which have thin flexible leaves and inhabit sheltered waters (Cambridge and Kuo, 1979). Both are infested by *Lynseia annae*. *Posidonia coriacea*, Kuo and Cambridge *P. ostenfeldii* den Hartog and *P. robertsoniae* Kuo and Cambridge are members of the *Posidonia ostenfeldii* species group characterised by narrower leaves, thicker in cross-section and inhabiting areas of stronger wave action (Kuo and Cambridge, 1984). Both are mined by *L. dianae* and the burrows are more difficult to detect than in the other species group of *Posidonia*. Seagrass workers in the Mediterranean, where *Posidonia* also exists, have not reported leaf miners.

Limnoriidae White comb. nov.

Limnoriadae White, 1850: 68.

Limnoriidae. — Cookson, 1991: 153 (modern diagnosis and synonymy).

Lynseiidae Poore, 1987: 258. — Bruce, 1988: 346 ff.

Diagnosis. Body semicircular in cross-section, elongate, 3–15 times as long as wide. Head more or less spherical, freely articulating with pereonite 1. Anterior margin of pereonite 1 directed upwardly or level with body, overlapping head posteriorly. Pleonites 1–5 free. Pleotelson with lateral crests. Antennae 1 contiguous, with scale (except *Lynseia himantopoda*). Antennae 2 lateral or ventrolateral to antenna 1. Eyes lateral. Frontal lamina absent. Clypeus transversely elongated, reaching lateral margin of antenna 2 articulation. Labrum circular. Mandible with palp 3-articulate or reduced to seta; incisors acute; lacinia mobilis small; spine row present (left spine row absent in *Lynseia dianae*); molar absent. Maxilla 1, outer lobe apex with 4–5 smooth lateral setae and 5 serrated medial setae.

Maxilla 2: inner lobe with simple setae plus large medial plumose oblique seta; 3–4 proximally plumose setae on middle lobe; 2 proximally plumose setae on outer lobe. Maxilliped narrow; epipod present; endite long. Pereopods ambulatory; carpus of pereopods 6 and 7 and often of others with distal comb-seta. Pereopod 1 propodus with 2 comb-setae posterodistally (thickened setae on *Lynseia dianae*). Pereopod 7 longer than other pereopods. Pleopods flabelliferan. Uropod ventrolateral; rami terminal, oval or circular in cross-section; exopod shorter than endopod, often with corneous apex.

Remarks. The diagnosis of the Limnoriidae given by Cookson (1991) is not seriously disrupted by the admission of the species of *Lynseia*, a genus previously assigned to its own family. The new diagnosis accommodates the greater elongation and narrowing of the body and some limbs found in *Lynseia*.

The differences between the Lynseiidae and Limnoriidae discussed by Poore (1987) are shown now not to be real. The two additional species of *Lynseia* share more features with species of *Limnoria* and *Paralimnoria* than does the unusual type species *Lynseia himantopoda*. Of the five apomorphies of *Lynseia* listed by Poore three are autapomorphies of *L. himantopoda*: lateral coxal plates fused to tergite, mandibular palp absent, loss of one ramus on pleopod 5. The reduced number of articles in the maxillipedal palp and elongate pereopods 6 and 7 are true for the genus but to a lesser extent in the new species.

The family Limnoriidae now includes three genera: *Limnoria*, *Paralimnoria* and *Lynseia*. Bruce (1988) originally tentatively placed his new genus and species *Hadromastax merga* in the Limnoriidae on the basis of head shape and articulation, antenna 1 and 2, mouthparts, pereopods and pleopods. Later Bruce and Müller (1991) removed *Hadromastax* to its own family recognised by several unique characteristics of the mandible, maxilla 1, maxillipedal epipod, free coxae 1, uropod, pereonite 1, and pleonal structure.

Phycolimnoria Menzies, 1957, initially a subgenus of *Limnoria* Leach, 1814, was synonymised with it by Cookson (1991) after a phylogenetic analysis.

Limnoria and *Paralimnoria* were diagnosed in detail by Cookson (1991), all 51 species were listed, all Australasian species described, and their biology and literature discussed.

Key to genera of Limnoriidae

1. Body more than 6 times as long as wide; pereopods 6 and 7 much longer than pereopod 5; mandibular palp of at most 1 minute article; maxillipedal palp of 1 or 3 articles .... *Lynseia* Poore

— Body less than 5 times as long as wide; pereopods 6 and 7 not significantly longer than pereopod 5; mandibular palp of 0–3 articles; maxillipedal palp of 5 articles 2

2. Uropodal rami elongate, both with corneous apex; antenna 1 flagellum of 5 articles; pereopod 1 secondary unguis trifid ....*Paralimnoria* Menzies

— Uropodal exopod much shorter than endopod, only exopod with corneous apex; antenna 1 flagellum with 4 or fewer articles; pereopod 1 secondary unguis bifid, simple or sometimes with spinules ....*Limnoria* Leach

See this work for a key to species of *Lynseia* and Cookson (1991) for keys to world species of *Paralimnoria* and *Limnoria*.

Lynseia Poore

Lynseia Poore, 1987: 259.

Diagnosis. Body 7–15 times as long as wide. Pleonite 1 epimeron square, extending ventrally as far as in other pleonites. Head longer than wide. Pleotelson elongate. Antenna 1 flagellum of 2–3 articles. Antenna 2 ventrolateral to antenna 1; flagellum of 1 article. Mandibular palp of 1-article or seta only; lacinia mobilis reduced (or absent on right mandible: *L. himantopoda* and *L. dianae*); lacking rasp and file (as are seen in *Limnoria*). Maxilla 1 outer lobe with 4 or 5 smooth similar apical spiniform setae. Lateral plates of coxae 2–7 posteriorly rounded. Pereopods with strong secondary unguis. Pereopods 6 and 7

elongate, pereopod 7 carpus as long or longer than basis. Pleopod peduncles without medial projection. Pleopod 5 with exopod reduced or absent, rami without plumose setae. Uropodal exopod less than half as long as endopod; endopod with 3 separate single or groups of brush setae. (Eggs almost as wide as body, carried in single longitudinal row.)

Remarks. *Lynseia* is most readily distinguished from *Limnoria* and *Paralimnoria* by its thin and elongate body shape, epimeron of pleonite 1 square and as long as epimeron 2 (short and acute in other genera), long pereopods 6 and 7 (especially the elongate carpus), reduced maxillipedal palp, reduced antennae 2 flagellum, and reduced pleopod 5 exopod. Pereopod 7 always points posteriorly, whereas in *Limnoria* it is often found anteriorly directed.

All species of *Lynseia* are small, rarely more than 2.5 mm long, and are found in burrows in the leaves of seagrasses. Rare specimens are found free-swimming in seagrass beds but the period spent moving between host plants is not known.

The genus is so far confined to southern and central western Australia; there have been no records from extensive seagrass beds in eastern Australia nor from other continents.

Key to species of *Lynseia*

1. Body 15 times as long as wide; pereopods 6 and 7 about 4 times as long as pereopod 4; maxillipedal palp of 1 article .... *Lynseia himantopoda*
— Body less than 9 times as long as wide; pereopods 6 and 7 less than 3 times as long as pereopod 4; maxillipedal palp of 3 articles 2
2. Pleotelson with strong lateral and anterior crests; uropodal exopod with corneous apex; mandibular palp of 1 article bearing 2 setae ....*Lynseia annae*
— Pleotelson without strong lateral and anterior crests, convex dorsally; uropodal exopod laminar; mandibular palp reduced to only 2 setae ....*Lynseia dianae*

Lynseia annae sp. nov.

Figures 1–3

Lynseia sp. 2. — Brearley and Walker, 1993: 417–425, fig. 1b.

Material examined. Holotype: Western Australia. Nancy Cove, Rottnest I. (32°0'S, 115°30'E), 3 m, *Posidonia sinuosa* leaves, A. Brearley, 12 Dec 1990, NMV J17242 (female, 1.45 mm).

Paratypes: collected with holotype, NMV J17246, (1 male, 2 slides); J17247 (1 male, 1 slide); J17248, (56 + 4 ovigerous females); J17245, (1 male, 3 slides). Thomson Bay, Rottnest I. (32°0'S, 115°33'E), 3 m, *Posidonia australis* leaves, A. Brearley, 22 Aug 1991, NMV J13247 (1 male, 1.6 mm, 2 slides), J13248 (48 specimens). S of Penguin I., Warnbro Sound (32°20'S, 115°43'E), 2 m, *Posidonia sinuosa* leaves, T. Evans, 11 Nov 1990, NMV J17243 (1 male, 1.55 mm, 1 slide), WAM 53-93 (3 males, 1.2–1.5 mm, 3 females, 1.8–2.1 mm). Cliff Head, Dongara (29°32'S, 114°59'E), 2.5 m, *Posidonia sinuosa* leaves, C. Manning, 27 Feb 1991 NMV J13245, (1 male, 1.58 mm, 3 slides), J13246 (11 specimens). Dunsborough, Geographe Bay (33°37'S, 115°18'E), 1 m, *Posidonia sinuosa* leaves, A. Brearley, 11 Jul 1991 NMV J13243, (1 immature, 2 slides). Geraldton, outside marina (28°46'S, 114°37'E), 9 m, *Posidonia sinuosa* leaves on rubble, T. Carruthers and G. Kendrick, 14 Aug 1991, WAM 54-93 (9 specimens).

South Australia, Ceduna (32°08'S, 133°41'E), 20 m off swimming beach, 1–1.5 m, *Posidonia australis* leaves, A. Brearley, 15 Jan 1993, NMV J31669 (8 specimens), WAM 57-93 (8 specimens).

Description. Body, pale yellow in preserved material, about 7 times as long as wide; pereonites shorter posteriorly; pleon about 0.4 of total length; pleonite 5 0.4 times as long as pleotelson. Pereonite 2 with fine anterodorsal transverse sculpture; pleonite 5 with minute dorsal tubercles. Pleotelson with concave oblique face about 1.4 times as long as wide, bordered by strong irregularly denticulate ridge laterally (lateral crests) to near midanterior margin; dorsal surface with partially fused pectinate scales; lateral surface anterior to base of uropod with fine vertical ridges; midposterior margin with scale spikes and vestigial sheathed setae between 2 larger stout setae.

Clypeus produced forward of antennae by distance equal to width of antenna 1 peduncle. Antenna 1 with small scale bearing 2 simple setae; second flagellar article with about 8 aesthetascs, third article with 1 aesthetasc and 3 simple setae. Antenna 2 about 0.6 times length of antenna 1; flagellum single article with 5 distal setae. Mandibular palp of 1 article bearing 2 apical simple setae; right mandible incisor with subapical tooth; lacinia mobilis small; spine row

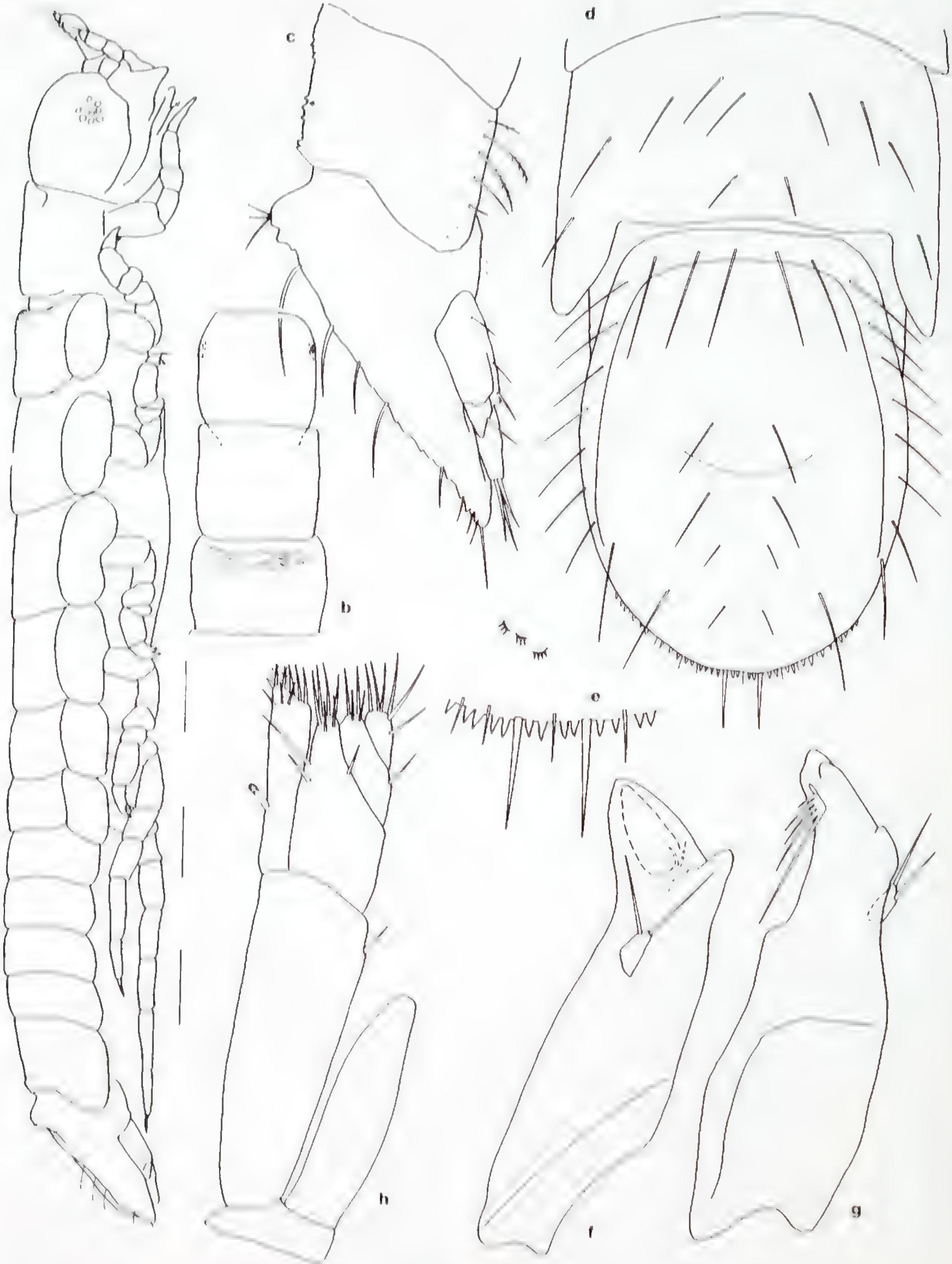

Figure 1. *Lynseia annae* sp. nov. a, habitus. b, head, pereonites 1 and 2. c, d, pleonite 5 and pleotelson. e, margin of pleotelson. f, g, left and right mandibles. h, left maxilliped. a, b, male, NMV J13245; c, e, female, NMV J17242; d, male, NMV J13247; f–h, male, NMV J17243. Scale lines = 0.1 mm.

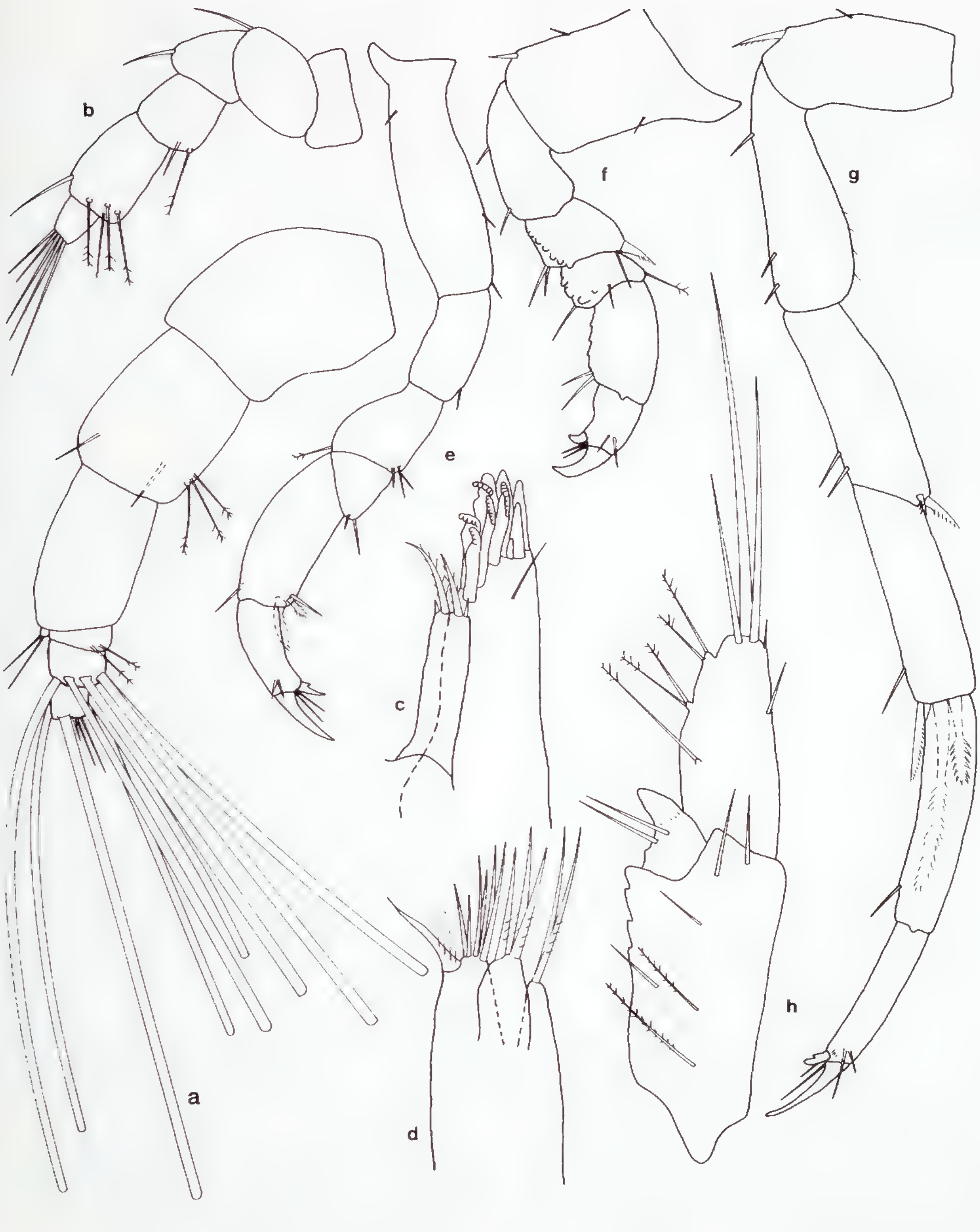

Figure 2. *Lynseia annae* sp. nov. a, b, antennae 1, 2. c, d, left maxillae 1, 2. e, f, g, pereopods 1, 4, 7. h, uropod. a–g, male, NMV J17245; h, female, NMV J17242.

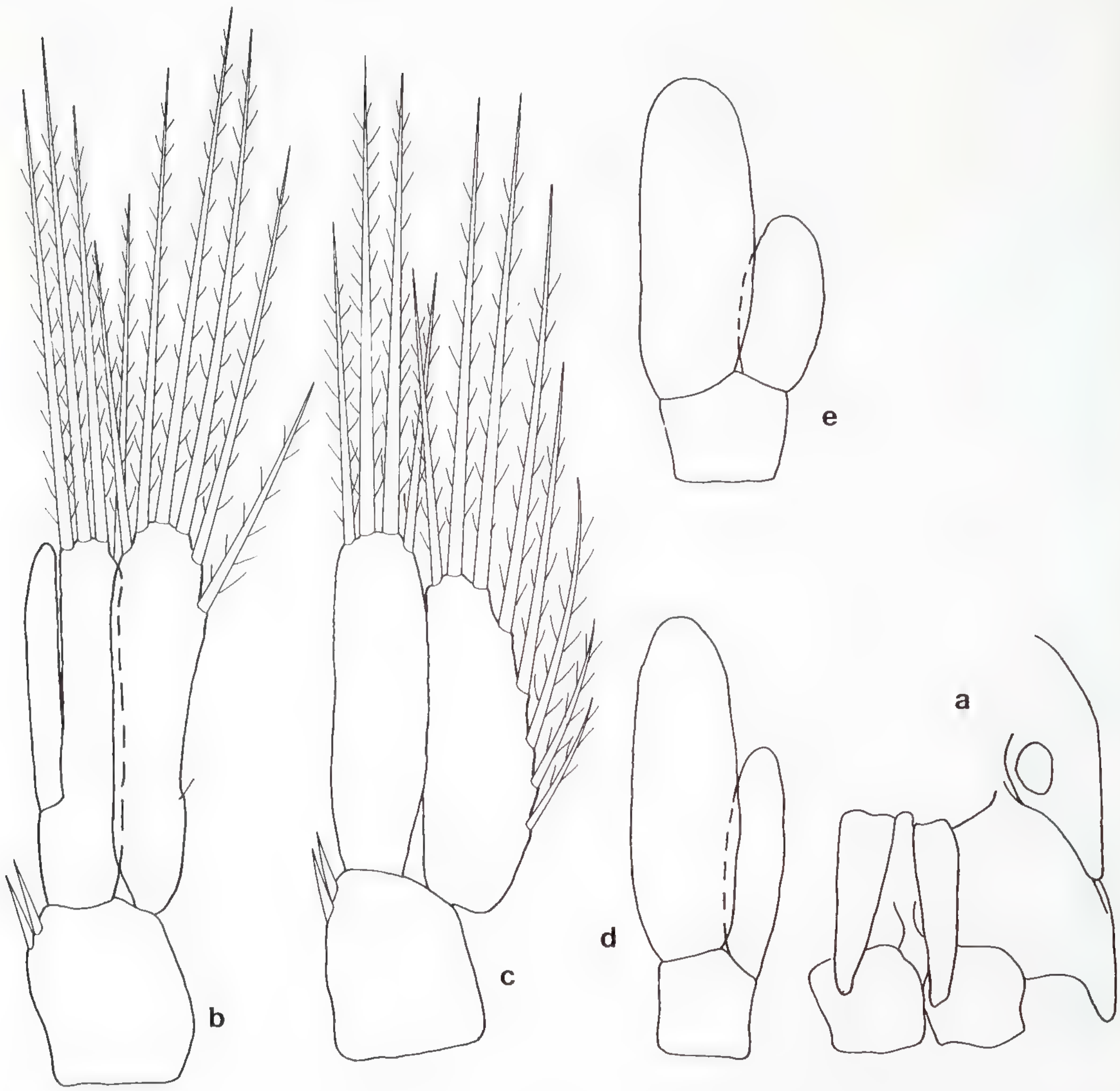

Figure 3. *Lynseia annae* sp. nov. a, pereonite 7 and pleonite 1 showing penes and peduncles of pleopods 1. b–e, pleopods 2, 4, 5 and 5. a, male, NMV J13245; b–d, male, NMV J17245; e, male, NMV J17246.

with 5 spines on right mandible, 2 on left. Maxilla 1: inner lobe with 2 short setae and 2 long plumose setae; outer lobe with 10 apical setae, mesial ones denticulate, one very short. Maxilla 2 inner lobe with 7 setae, medial one long; middle and outer lobes shorter than inner lobe, with 3 and 2 setae respectively. Maxillipedal epipod elongate, 3.7 times as long as wide, not reaching base of palp, without setae; palp reaching as far as endite, of 3 articles; endite with 3 curved pappose setae lateral to 2 distomedial pappose setae, with coupling hook.

Coxae 2–7 with clear lateral sutures. Pereopod 4 shortest; pereopod 1 1.3 times as long, pereopod 5 1.4 times as long, pereopod 6 2.0 times as long, and pereopod 7 2.2 times as long as pereopod 4. Secondary unguis of pereopods 1 and 7 bifid. Pereopod 7 carpus with 3 comb-setae.

Penes 4 times as long as width at base, tapering, separate, attached to posterior margin of ventral plate of pereopod 7.

Oostegites on pereopods 3 and 4.

Pleopod 1 with 3 coupling hooks, pleopods 2–4 with 2 coupling hooks. Exopod plumose setae

mostly apical on pleopods 1 and 2, apical and lateral on pleopods 3 and 4. Pleopod 2 with plumose setae up to 1.3 times as long as exopod; appendix masculina reaching endopod tip, articulating proximal to midlength of endopod, apically rounded. Pleopod 5 with 2 rami, articulation of endopod anterior to exopod, exopod about 0.6 times as long as endopod, endopod 0.9 times as long as endopod of pleopod 2, peduncle without lateral seta.

Uropodal peduncle with posterolateral tubercles; endopod 0.7 times as long as peduncle; exopod 0.4 length of endopod with 1+2+2 brush setae laterally, with corneous apex.

Etymology. For Anne Brearley, whose work on the biology of these isopods has discovered so much.

Distribution. Geraldton, Western Australia, to Ceduna, South Australia; from burrows in leaves of *Posidonia australis* and *P. sinuosa*; to 9 m depth.

Remarks. *Lynseia annae* is immediately recognisable from its body proportions and the pleotelson which develops lateral and anterior crests in more mature specimens. Other diagnostic characters are the corneous apex on the uropod exopod, lack of a seta on the maxilliped epipod, the large separate penes, three coupling hooks on pleopod 1, only 2 large pappose setae on the inner lobe of maxilla 1, and mandibular palp of one article. The rami of pleopod 5 were narrower in one of the individuals dissected than the other (Fig. 3d, e).

The ornamented pleotelson was usually held strongly inclined to the remaining body, apparently to obstruct the burrow. In seagrass leaves they were often found in pairs, with female deeper in the burrow. The animal was seen mostly with its lateral margins touching the thinnest surface of the leaves, feeding only on the mesophyll cells between the epidermis of the emergent leaf. Up to 75% of leaves were burrowed at Rottnest I. Burrows may branch and minor branches contained smaller individuals (Brearley and Walker, 1993).

Four ovigerous females were found, all with eggs in a single longitudinal row (3–4 eggs each). In *Limnoria* and *Paralimnoria* there are usually several eggs abreast.

The species has a wide distribution in central and south-eastern Western Australia and has been found in western South Australia. The species was not found in searches in Shark Bay, Western Australia nor near Sydney, NSW where *P. australis* exists (A. Brearley, pers. comm.).

Lynseia dianae sp. nov.

Figures 4, 5

Lynseia sp. 3. — Brearley and Walker, 1993: 417, 424–425.

Material examined. Holotype: Western Australia, Lal Bank, off Marmion, Perth (31°50'S, 115°45'E), 4 m, *Posidonia coriacea* leaves, C. Manning, 13 Mar 1991, NMV J17253 (male, 1.9 mm).

Paratypes: collected with holotype, NMV J13238 (1 female with embryo), J13239 (1 male, 1.95 mm), J17251 (1 male, 2.0 mm, 1 slide), J17252 (1 female, 1.8 mm, 1 slide), J17254 (10 males, 1.6–2.0 mm; 19 females and juveniles, largest 2.6 mm). Bremer Bay (34°24'S, 119°26'E), *Posidonia ostenfeldii* leaves, T. Carruthers, 3 Jun 1991, NMV J17249 (1 male, 1.85 mm, 1 slide), J17250 (2 males, 1.5–1.9 mm, 7 females, 1.6–2.3 mm). Little Boat Harbour, Bremer Bay (34°24'S, 119°26'E), *Posidonia robertsoniae* leaves, T. Carruthers, 12 Jan 1992, WAM 52-93 (8 specimens).

Description. Body, pale yellow in preserved material, about 8–9 times as long as wide; pereonites shorter posteriorly; pleon about 0.4 of total length. Pleonite 5 0.5 length of pleotelson. Pereon generally smooth. Pleotelson mid-dorsally convex, with lateral crests weakly raised; dorsal surface structure without scales, posterior margin without setae or scale spikes.

Clypeus produced forward of antennae by distance equal to width of antenna 1 peduncle. Antenna 1 with minute scale or absent; flagellum of 2 articles, second article with about 4 aesthetascs and 3 simple setae. Antenna 2 about 0.85 times as long as antenna 1; flagellum single article with 5 distal setae. Mandibular palp lacking, replaced by 2 simple setae; right incisor with subapical tooth; lacinia mobilis absent; spine row with 6–8 spines on right, absent on left. Maxilla 1 inner lobe with 3 plumose setae; outer lobe with 9 apical setae. Maxilla 2 inner lobe with 6 simple setae plus longer oblique plumose seta, middle and outer lobes as long as inner lobe, with 4 and 2 setae respectively. Maxillipedal epipod elongate, 5 times as long as wide, not reaching base of palp, with 1 seta; palp reaching as far as endite, with 3 articles; endite with 3 curved pappose setae lateral to 2 distomedial pappose setae, with coupling hook.

Coxae 2–7 with clear lateral sutures. Pereopod 1 propodus with 2 posterodistal comb-setae or 2 basally thickened simple setae. Pereopod 4 shortest; pereopod 1 1.7 times as long, pereopod 5 2.3 times as long, pereopods 6 and 7 2.7 times as long as pereopod 4. Secondary unguis of

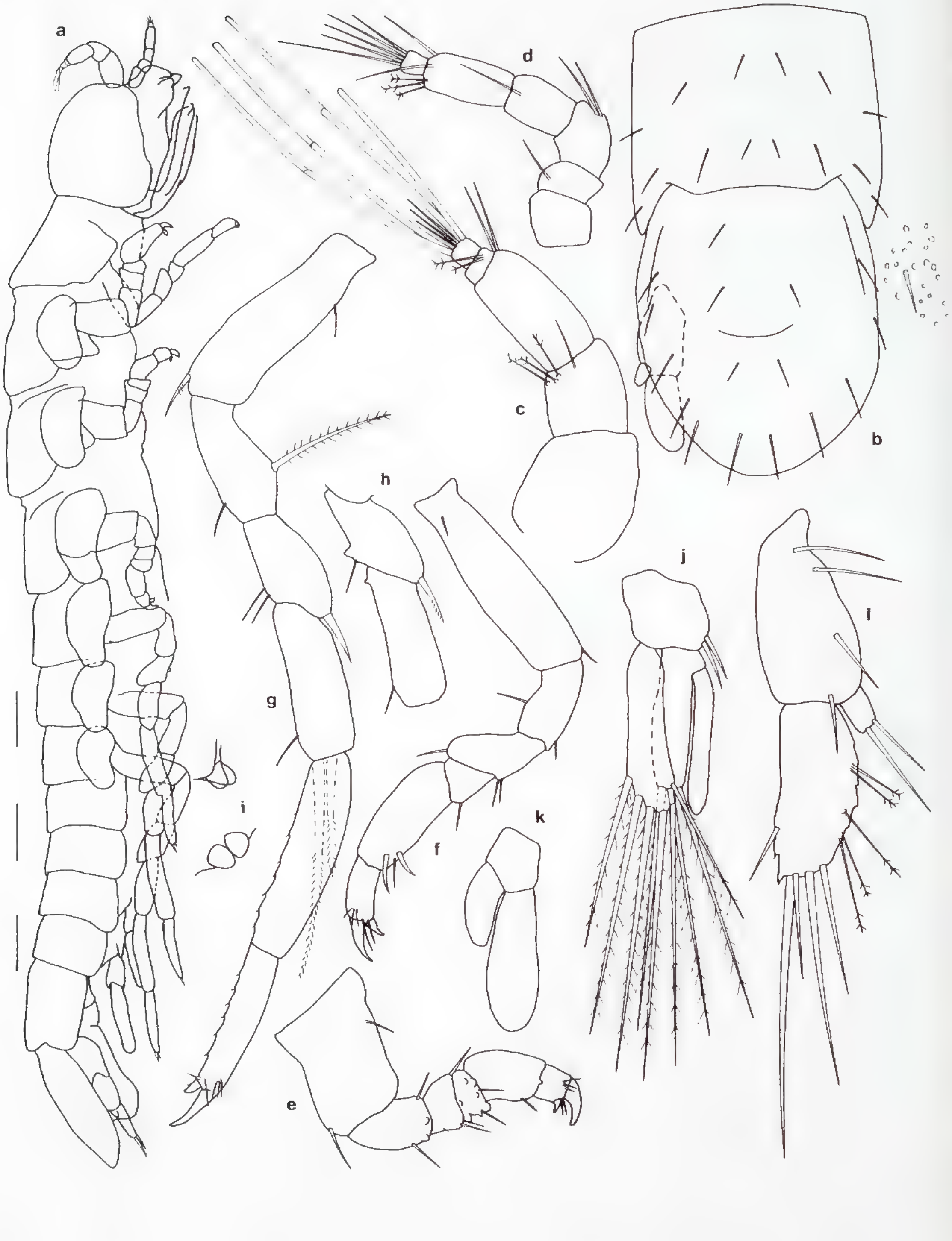

Figure 4. *Lynseia dianae* sp. nov. a, habitus. b, pleonite 5 and pleotelson (plus detail of surface). c, d, antennae 1, 2. e, f, g, pereopods 1, 4, 7. h, merus and carpus of pereopod 7. i, penes, lateral and ventral views. j, k, pleopod 2, 5. l, uropod. a, i, male, NMV J13239; b, e–g, j, l, male, NMV J17251; c, d, h, male, NMV J17249; k, female, NMV J17252. Scale lines = 0.1 mm.

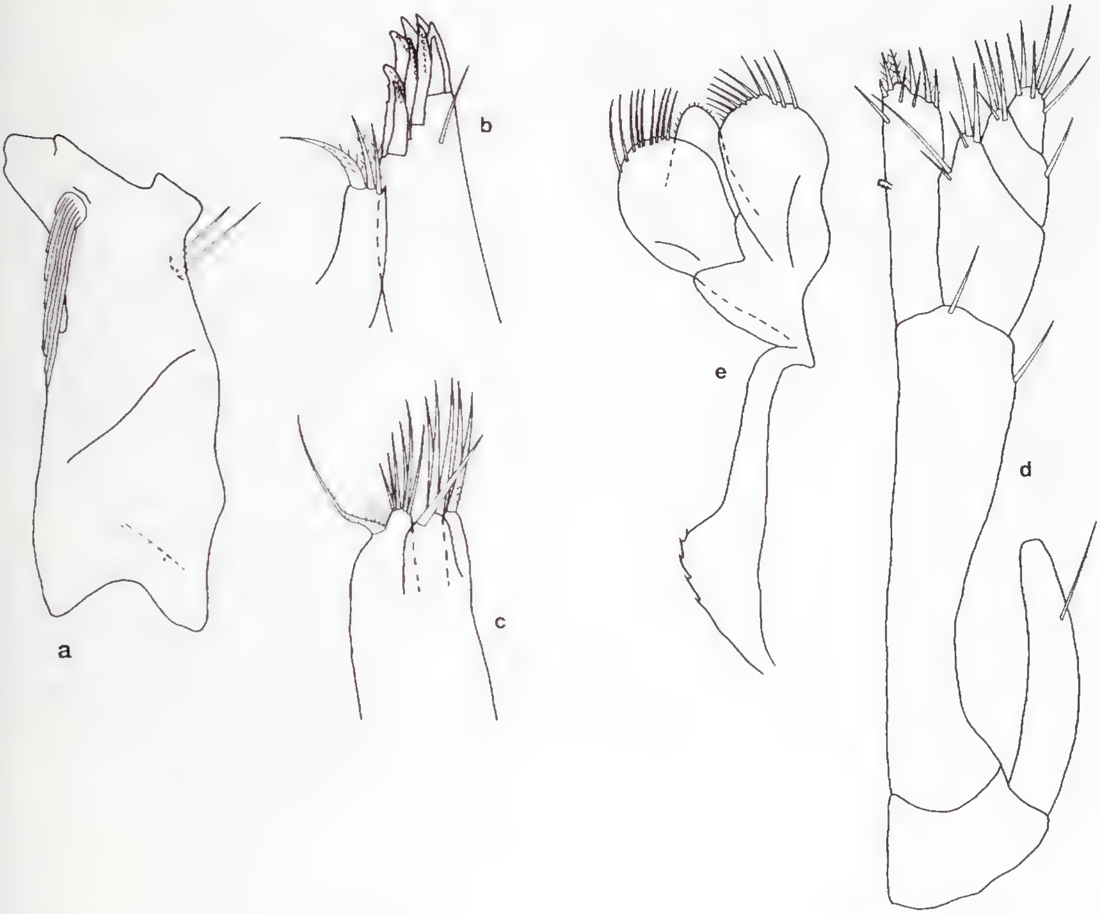

Figure 5. *Lynseia dianae* sp. nov. a, right mandible. b, c, left maxillae 1, 2. d, left maxilliped. e, labium. a–e, male, NMV J17251; e, male, NMV J17249.

pereopods 1 and 7 simple, with posterior setule. Pereopod 7 carpus with 2–3 comb-setae, merus and carpus with or without tubercle. Ischium of pereopods 5–7 with large anterior plumose seta.

Penes short, less than twice as long as broad, separate but contiguous.

Oostegites on pereopods 3 and 4.

Pleopods 1–4 with 2 coupling hooks. Exopod plumose setae mostly apical on pleopods 1 and 2, apical and lateral on pleopods 3 and 4. Pleopod 2 with plumose setae up to 1.5 times as long as exopod; on male appendix masculina reaching beyond endopod tip, articulating proximal to midlength of endopod. Pleopod 5 with 2 rami, articulation of endopod anterior to exopod, exopod about 0.5 times as long as endopod, endopod 0.9 times as long as endopod of pleopod 2, rami without setae.

Uropod peduncle without posterolateral tubercles; endopod 0.9 times as long as peduncle; exopod 0.2 length of endopod, laminar, with 2 apical setae.

Etymology. For Diana Walker whose concern for the health of seagrasses has led to the discovery of these two new species.

Distribution. South Western Australia, from Perth to Bremer Bay; in burrows in leaves of *Posidonia coriacea*, *P. ostenfeldii* and *P. robertsoniae*.

Remarks. The key feature separating *Lynseia dianae* from *L. annae*, which has only slightly more elongate form, is the shape of the pleotelson; well developed lateral crests are absent and the dorsal area is slightly convex. In addition, it differs in possessing a simple secondary unguis on pereopod 1, lacking setae and scale spikes on

the posterior margin of the pleotelson, possessing a simple seta on the maxilliped epipod, only two coupling hooks on pleopod 1, having a laminar uropodal exopod, having three plumose setae on the inner lobe of maxilla 1, and in lacking a mandibular palp.

Lynseia dianae differs from both other species by: large plumose seta on ischium of pereopods 5–7, longer basis on pereopod 7, narrow maxilliped epipod, very short separate penes, only two flagellar articles on antenna 1, and four setae on the middle lobe of maxilla 2.

It differs from *L. himantopoda* in having a coupling hook and more apical setae on the maxillipedal endite, three not one articles on the maxillipedal palp, pleopods 3–4 with both lateral and apical plumose setae, pleopod 5 with two rami.

On some specimens examined (from slides and in situ), the antennal scale was detected while in others it was so small that it could not be certain that it was separate from the peduncle. One ovigerous female carried a single embryo 0.23 the length of the whole animal, in two pairs of oostegites on pereopods 3 and 4.

Only 17% of leaves of the host plants at Marmion were mined (Brearley and Walker, 1993).

Lynseia himantopoda Poore

Figure 6

Lynseia himantopoda Poore, 1987: 259–263, figs 1–4. — Brearley and Walker, 1993: 417, 420, 425.

Material examined. Victoria. Rhyll spit, Phillip I. (38°28'S, 145°19'E), artificial seagrass, G. Edgar, 29 Sep 1991 NMV J13099 (6 specimens).

South Australia. Port Macdonnell Pier (38°03.5'S, 140°42.1'E), 0.5 m, *Heterozostera tasmanica* leaves, G. C. B. Poore and R. S. Wilson, 13 May 1990 (stn CRUST 81), NMV J20403 (1 male).

Western Australia. Thomson Bay, Rottnest I. (32°0'S, 115°33'E), 2 m, *Heterozostera tasmanica* leaves, A. Brearley, 23 Jan 1991, WAM 58-93 (17 specimens). Princess Royal Harbour, E side (35°03'S, 117°53'E), 1.5 m, *Posidonia* leaves, G. Edgar, 28 Jan 1991, NMV J21806 (1 male).

Distribution. Southern coast of Australia, central Victoria to region of Perth, Western Australia; burrows in leaves of *Heterozostera tasmanica*; to about 2 m depth.

Remarks. New material extends the range of this species to southern Western Australia where it is confined to *Heterozostera tasmanica* as it is in the eastern states. Brearley and Walker (1993) recorded 38% of leaves with burrows near the leaf sheath at Rottnest I. The burrows were

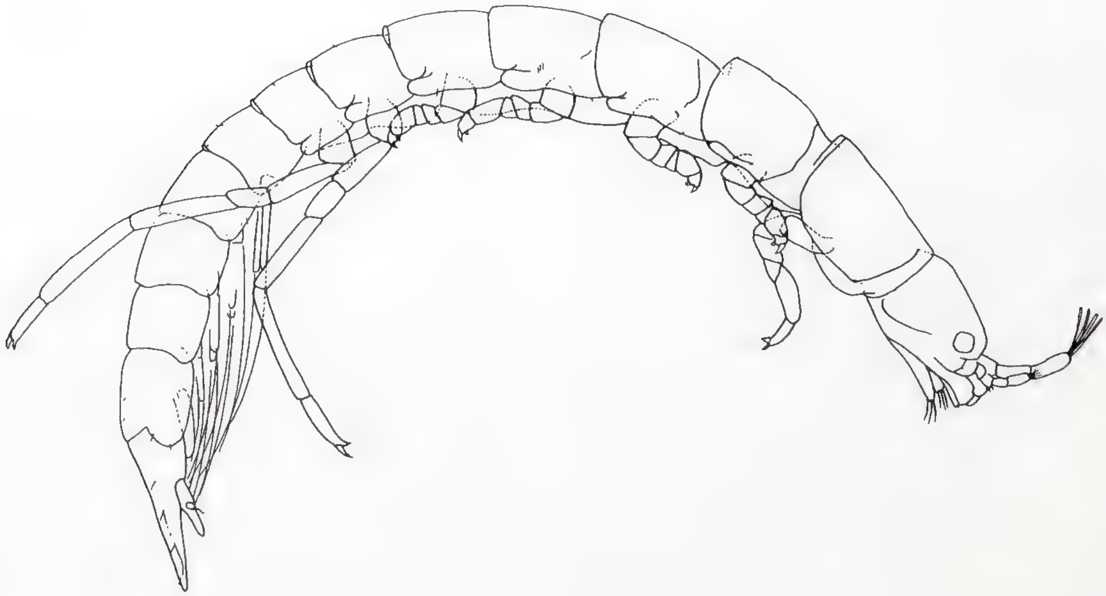

Figure 6. *Lynseia himantopoda* Poore, 1987. Habitus (from Poore, 1987).

confined to mesophyll tissue, the epidermis being untouched.

Dissection of new material showed that it does have an inner lobe on maxilla 1 like that in other species (not figured by Poore, 1987) and confirmed the absence of exopod on pleopod 5.

Acknowledgements

We are especially grateful to Di Walker and Anne Brearley, Department of Botany, University of Western Australia, for bringing these animals to our attention. We appreciate Anne Brearley's generosity in allowing us access to her research results. We thank Niel Bruce for comments on the systematics of this group and to Luke Flood who inked the figures.

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Memoirs of the Museum of Victoria 54: 191–205 (1994)

A REVIEW OF THE GENUS *PARANYCTIOPHYLAX* TSUDA FROM SULAWESI, PAPUA NEW GUINEA AND NORTHERN AUSTRALIA (TRICHOPTERA: POLYCENTROPODIDAE)

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Abstract

Neboiss, A., 1994. A review of the genus *Paranyctiophylax* Tsuda from Sulawesi, Papua New Guinea and northern Australia (Trichoptera: Polycentropodidae). *Memoirs of the Museum of Victoria* 54: 191-205.

The genus *Paranyctiophylax* Tsuda in Sulawesi, Papua New Guinea, Bougainville Island and northern Australia is reviewed. Eleven new species are described, definitions of several established species are revised and distributional data added.

Introduction

Disparities within the genus *Nyctiophylax* Brauer, 1865, were discussed by Neboiss (1993) who redefined the genus and transferred 25 of its species to *Paranyctiophylax* Tsuda, 1942. The distribution of *Paranyctiophylax*, previously known only from Japan, was thus expanded into South-east Asia, New Guinea and Australia (Fig. 1) with a further three distinct species groups in Sri Lanka, Africa and North America. Six new species of *Paranyctiophylax* are described here from northern Australia, two from the Indonesian island of Sulawesi, two from Papua New Guinea and one from Bougainville I., which is the eastern-most occurrence of the genus. Other species are known from the Bassian province of south-eastern Australia (Neboiss, 1981) but this is south of an extensive faunal barrier created by a stretch of dry savannah south of Townsville (Keast, 1961) and consideration of these species is outside the scope of this paper.

The two east Asian species, *P. kisoensis* Tsuda and *P. digitatus* (Martynov), are distinct from the species from Sulawesi, New Guinea, northern Australia and Bougainville I. In the east Asian species the phallus is firm, distally protruding, and apically rounded, without internal spines. The known species from the Sunda Is to northern Australia are all characterised by having the phallic apparatus soft and membranous, generally retracted into the genitalic capsule. The phallus is more or less expandable and contains a set of internal chitinous spines or rods, the particular arrangement of which is species specific.

Sixteen species are discussed or described in this paper. Revised definitions are given for the two east Asian species, new records are added to distributions of one New Guinean and one Australian species and 11 new species are described.

The east Asian species are *P. kisoensis* Tsuda from Japan (type species) and *P. digitatus* (Martynov) from Russia (Eastern Siberia).

The Sunda Islands – northern Australian species are *P. apicatus* sp. nov., Australia, Cape York; *P. basispinosus* sp. nov., Australia, North Queensland; *P. dicellatus* sp. nov., Australia, North Queensland; *P. eidolonus* sp. nov., Australia, North Queensland; *P. flavus* (Ulmer), Papua New Guinea; *P. gyratus* sp. nov., Papua New Guinea; *P. icelus* sp. nov., Indonesia, Sulawesi Tenggara; *P. kabaensis* sp. nov., Indonesia, Sulawesi Tenggara; *P. lumarius* (Neboiss), Indonesia, Sulawesi Utara; *P. parvus* (Mosely), Australia, Northern Territory; *P. rhamphodes* sp. nov., Australia, Northern Territory; *P. synorius* sp. nov., Bougainville Island; *P. spiculatus* sp. nov., Australia, North-west Australia; and *P. traunensis* sp. nov., Papua New Guinea.

Material and methods

All specimens are preserved in 75% ethanol unless stated otherwise. Illustrations have been prepared from abdomens cleared in cold KOH solution, then transferred to glycerol for drawing and later storage in microvials. Drawings of genitalia were made with the assistance of a camera lucida mounted on a Wild M20 compound microscope and wings were prepared as temporary microscope mounts in glycerol and drawn from a Wild M8 dissecting microscope with the aid of a camera lucida. The wing colours in all specimens preserved in alcohol show various degrees of fading. All dissected specimens are identified by the author's notebook number with prefix PT on a yellow label.

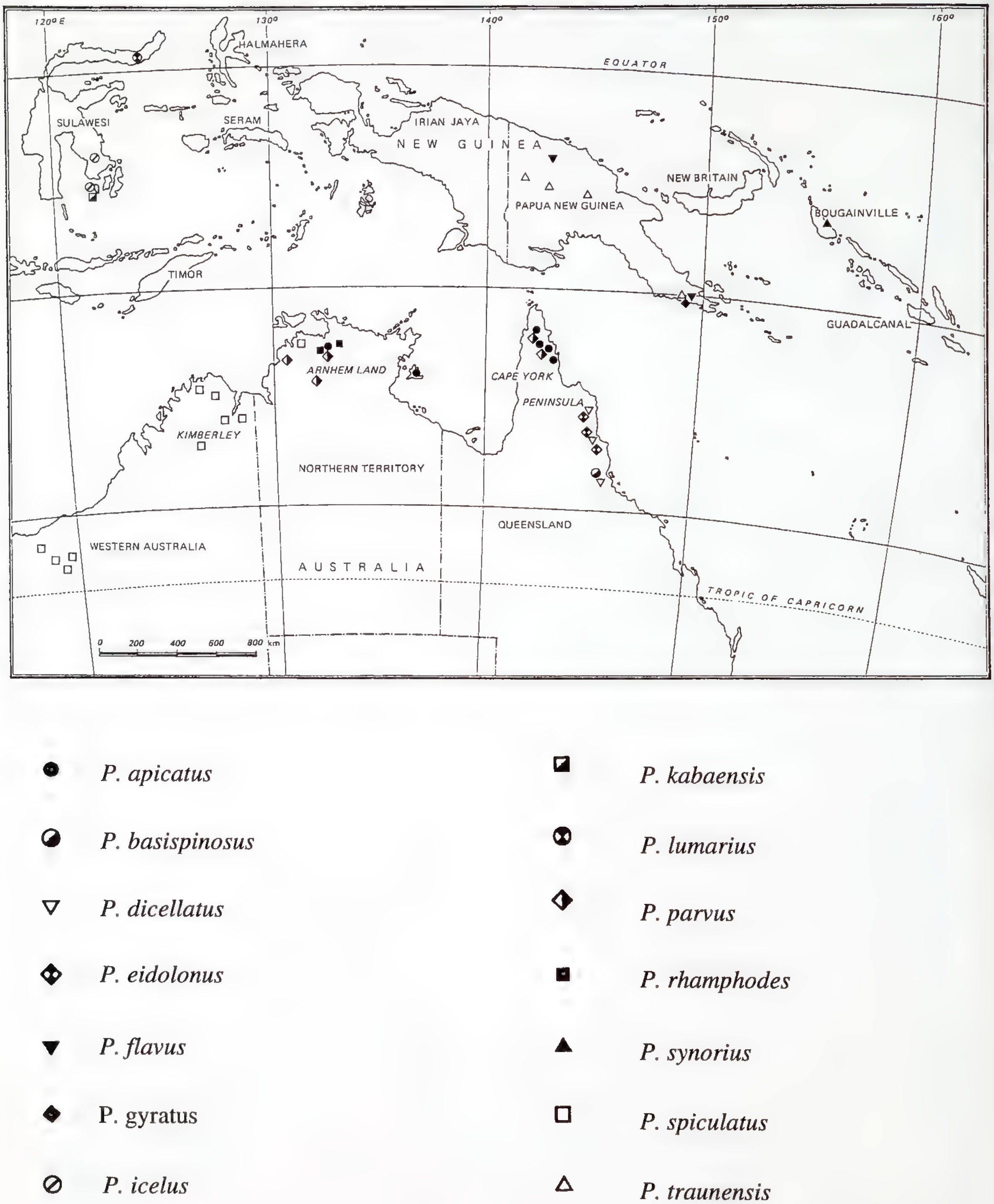


Figure 1. Distribution of *Paranyctiophylax* species described in this paper.

The following abbreviations have been used to designate the depository institutions: ANIC, Australian National Insect Collection, Canberra, Australia; BPBM, Bernice P. Bishop Museum, Honolulu, USA; NMV, Museum of Victoria, Melbourne, Australia; NTMD, Northern Territory Museum, Darwin, Australia; QM, Queensland Museum, Brisbane, Australia; RMNH, National Natural History Museum, Leiden, The Netherlands; UOJ, University of Osaka, Japan; ZMSP, Zoological Museum, State University, St Petersburg, Russia.

Paranyctiophylax Tsuda

Paranyctiophylax Tsuda, 1942: 265. — Neboiss, 1993: 108.

Type species. Paranyctiophylax kisoensis Tsuda, 1942 (by original designation).

Revised generic diagnosis. Fore wing cross-vein C-Sc basad of base of discoidal cell, fork 1 absent, fork 3 present, petiolate, anal veins looped, junction of A2 and A3 close to or merged with junction to Al; hind wing forks 1 and 3 absent (aberrantly a small fork 3 may be present), discoidal cell short, triangular, cell at base of anal veins A2 and A3 extended towards wing margin, cross-vein closing cell distinctly spearated from cross-vein Cu2-A1.

Male genitalia with superior appendages moderately large, arising distad of upper angle of sternite IX; paraproctal processes conspicuous, robust, directed posteriorly or curved ventrad; inferior appendages moderately long, slender, curved dorsad.

Female genitalia with tergite VIII large, sternite VIII broad, ventral plates attached basolaterally.

EAST ASIAN SPECIES

Diagnostic features. Apex of phallus protruding distally, firm, tip rounded, internal spines absent, with or without parameres.

Paranyctiophylax kisoensis Tsuda, 1942

Figures 2, 3

Paranyctiophylax kisoensis Tsuda, 1942: 265. — Neboiss, 1993: 108.

Type material. 6 ♂ Japan, Otakigawa-hontani, Kiso, Nagano, 4 Aug 1939, M. Tsuda (type not seen).

Material examined. 1♂, Japan, Jadani, Hakusan, 31 Aug 1981, K. Tanida (UOJ).

Revised diagnosis. Colour blackish-brown, wing venation as in Fig. 3. Length of fore wing ♂ 6.5–6.7 mm.

Male genitalia (Fig. 2) with sternite IX small, in lateral view about as long as high without mesoventral projection; superior appendages robust, subtriangular; paraproctal processes short, broad at base, apex rounded; inferior appendages moderately robust. Phallus protruding distally, apex firm, dark blackish-brown.

Female not described.

Distribution. Japan.

Remarks. This species is distinguished from *P. digitatus* by the presence of parameres and the shapes of sternite IX, the superior appendages and the paraproctal processes.

Paranyctiophylax digitatus (Martynov, 1934)

Figure 4

Nyctiophylax digitatus Martynov, 1934: 241.
Paranyctiophylax digitatus. — Neboiss, 1993: 108.

Type material. Holotype ♂, Russia, South Ussurian Kray, Vinogradovka, 5 Jul 1929, Kirichenko (ZMSP) (examined). Paratype 1♂ collected with holotype (♂ genitalic prep. PT–1967 figured).

Revised diagnosis. Colour in dry specimen greyish-brown, distinct pale hyaline angular spot at base of median cell. Length of fore wing ♂ 6.0 mm; (length of body 4–4.5 mm given by Martynov).

Male genitalia (Fig. 4) with sternite IX in lateral view about as long as high with stout mesoventral projection; superior appendages short, bluntly rounded apically; paraproctal processes short, rather broad, only slightly broader at base, apex truncate; inferior appendages slender, pointed apically, with basal elbow slightly produced. Phallus protruding distally beyond superior appendages, apex firm, dark blackish-brown.

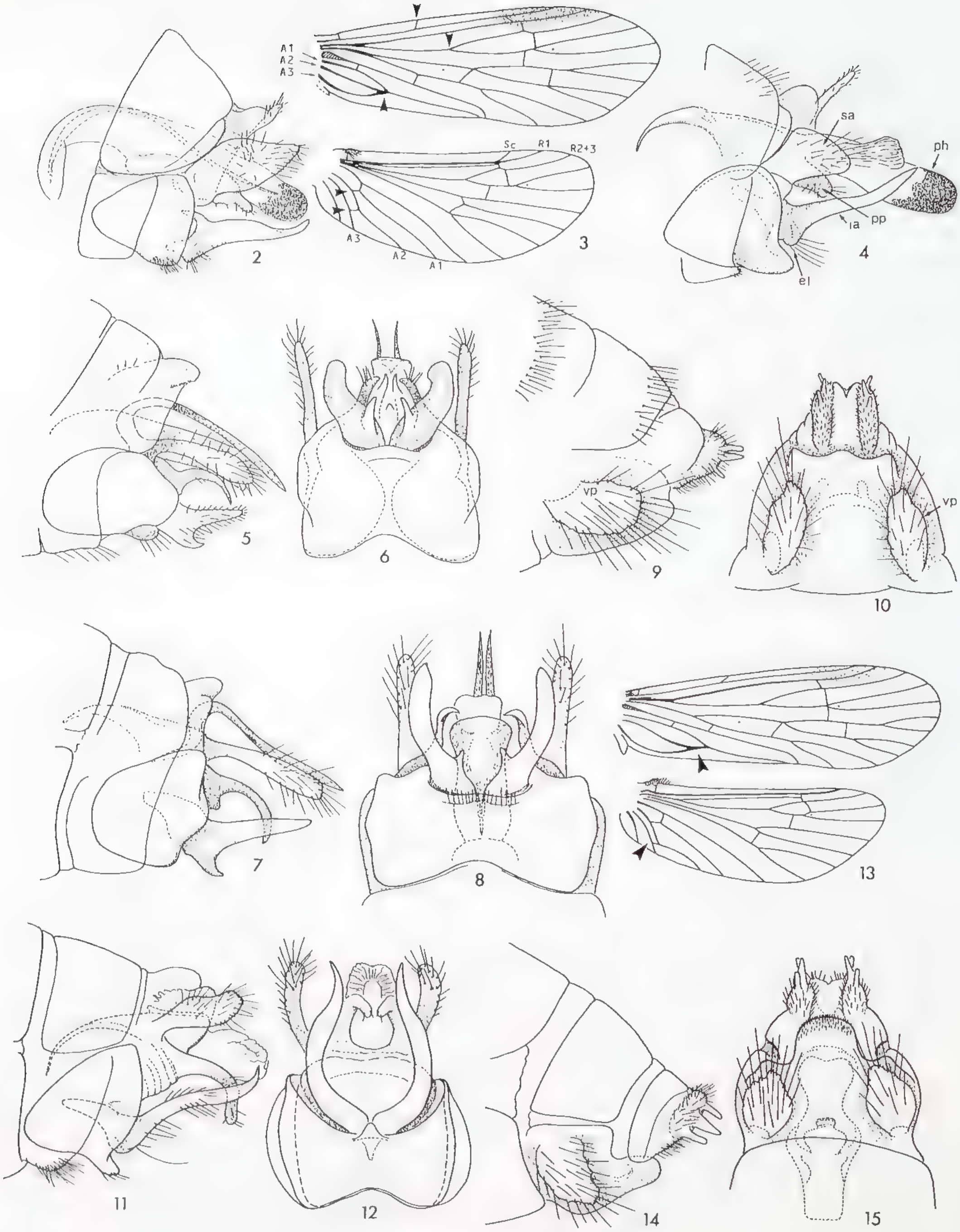
Female: In the original description the female is noted as having 'end of abdomen blackish', but no female specimens are included in the type material.

Distribution. Russia (Siberian far south-east).

Remarks. Males of this species are distinguished from *P. kisoensis* by the smaller superior appendages, the apically truncate paraproctal processes and the shape of sternite IX.

THE SUNDA ISLANDS - NORTHERN AUSTRALIAN SPECIES

Diagnostic features. Phallic apparatus membranous, not protruding distally; with internal or sometimes external chitinous spines or rods; parameres absent.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Paranyctiophylax lumarius (Neboiss, 1989)

Figures 5, 6

Nyctiophylax lumarius Neboiss, 1989: 107.
Paranyctiophylax lumarius – Neboiss, 1993: 108.

Type material. Holotype ♂, Indonesia, Sulawesi Utara, Dumoga Bone National Park, Edwards camp near Tumpah R., 00°35'N, 123°51'E, 650m asl, 22 May 1985, A. Wells (NMV). Paratypes: 10♂ collected with holotype (♂ genitalic prep. PT–1558 figured) (NMV, RMNH).

Distribution. Indonesia, Sulawesi Utara.

Remarks. The statement in the original description (Neboiss, 1989) that the 'preanal appendages are formed by three processes' requires amendment. The three processes arise separately, and of these the middle processes should be regarded as superior appendages. The upper processes arise from the upper inner margin of sternite IX, rapidly curve mesad and then distad just above the phallus and may correspond to the intermediate appendages (Holzenthal and Hamilton, 1988). The lower processes correspond to the paraproctal processes of species like *P. icelus*, however, in *P. lumarius* they are not fused mesally below the phallus. The inferior appendages show similarities to *P. hjangsanchonus* (Botosaneanu, 1970) of Korea but the form of the superior appendages is distinct. The female is unknown. No new material was available for study.

Paranyctiophylas kabaensis sp. nov.

Figures 7–10

Type material. Holotype ♂, Indonesia, Sulawesi Tenggara, Pulau Kabaena, 4km S of Tangkeno, 05°18'S, 121°57'E, 300m asl, 4 Nov 1989, at light, R. de Jong and J. Huisman (site JS 8932) (RMNH). Paratypes: 2♂s, 1♀ collected with holotype (RMNH, NMV) (♀ genitalic prep. PT–1961 figured); 1♂ same locality 5 Nov 1989, at light (site JS 8933); 1♂ same locality 7 Nov 1989, at light (site JS 8937) (RMNH); 3♂ 3♀ Sulawesi Tenggara, Pulau Kabaena, Batuawu, 05°25'S 121°48'E, 11 Nov 1989, at light, R. de Jong and J. Huisman (site JS 8945) (RMNH, NMV) (♂ gentalic prep. PT–1956 figured).

Description. Colour blackish-brown, similar in both sexes. Length of fore wing ♂ 3.5–4.3mm; ♀ 4.3–5.1mm.

Male genitalia (Figs 7, 8) similar to *P. lumarius* but differs in details. Abdominal sternite IX in lateral view about as long as high; superior appendages slender, somewhat obliquely truncate apically, paraproctal processes strongly curved dorsad, pointed apically. Inferior appendages more slender than in *P. lumarius*, pointed apically, mesoventral branch small. Phallus without internal bars or spines.

Female genitalia (Figs 9, 10) sternite VIII apically broad, distal margin shallowly trilobed.

Etymology. Reference to the type locality.

Remarks. This species is very similar to *P. lumarius* but may be distinguished by the details of male genitalia, particularly the more elongate inferior appendages.

Paranyctiophylax icelus sp. nov.

Figures 11–15

Type material. Holotype ♂, Indonesia, Sulawesi Tenggara, Pulau Kabaena, 1km S of Tangkeno, riverine forest, Sungai Lantinoli, 05°17'S, 121°57'E, 8 Nov 1989, at light, R. de Jong and J. Huisman (site JS 8939) (RMNH). Paratypes: 50 ♂, 1♀, collected with holotype (BPBM; NMV; RMNH) (♂ genitalic prep. PT–1911 figured); 5♂, 1♀, same locality 9 Nov 1989, (site JS 8940–42) (RMNH); 10♂, 25♀, 4km S of Tangkeno, 4 Nov 1989, R. de Jong and J. Huisman (site JS 8932) (BPBM; NMV; RMNH) (♀ genitalic prep. PT–1957 figured); 15♂, 4♀, same locality 5 Nov 1989 (site JS 8933) (RMNH).

←

Figures 2, 3, *Paranyctiophylax kisoensis*, 2, male genitalia lateral; 3, male wing venation.
Figure 4, *P. digitatus*, male genitalia lateral.
Figures 5, 6, *P. lumarius*, 5, male genitalia lateral; 6 male genitalia ventral.
Figures 7–10, *P. kabaensis*: 7, male genitalia lateral; 8, male genitalia ventral; 9, female genitalia lateral; 10, female genitalia ventral.
Figures 11–15, *P. icelus*: 11, male genitalia lateral; 12, male genitalia ventral; 13, male wing venation; 14, female genitalia lateral; 15, female genitalia ventral.
ia, inferior appendage; el, elbow of inferior appendage; ph, phallus; pp, paraproctal process; sa, superior appendage; vp, ventral plate.

Other material examined. Indonesia, Sulawesi Tenggara, 6 ♂, 3km S of Tangkeno, Pulau Kabaena, 350m asl, 6 Nov 1989 (site JS 8936) (RMNH); 1♂, same locality 7 Nov 1989 (site JS 8938) (RMNH); 2♂, 1♀, same locality 5 Nov 1989 (site JS 8934) (RMNH); 9♂, 7♀, N slope Gunung Watuwila, Mokowo R., 03°48'S, 121°39'E, 250–1100m asl, 11–19 Oct 1989 (site JS 8902) R. de Jong and J. Huisman (NMV; RMNH).

Description. Fore wing with median cell closed, venation as in Fig. 13. Length of fore wing: ♂ 4.0–4.6mm; ♀ 4.4–5.3mm.

Male genitalia (Figs 11, 12), abdominal sternite IX in lateral view short, subtriangular, with distomesal projection; superior appendages elongate, slender; paraproctal process long, curved ventrad, apices bluntly rounded; inferior appendages slender, pointed apically. Phallus with small internal chitinous spine.

Female genitalia (Figs 14, 15) ventral plates small, sternite VIII, in ventral view with broad, rounded mesal lobe.

Etymology. From *ikelos* (Greek), 'like' refering to the similarity of species in Australia.

Remarks. The species is distinguished from other Sulawesi species by the slender inferior appendages, acute apically, and by the shape of superior appendages.

Paranyctiophylax parvus (Mosely)

Figures 16–19

Nyctiophylax parvus Mosely in Mosely and Kimmins, 1953: 357, fig. 246.

Paranyctiophylax parvus. — Neboiss 1993: 108.

Type material. Holotype ♂, Australia, Northern Territory, Manbulla Station (=Manbulloo) 14°31'S, 132°12'E, 19 Jul 1929, Mackerras and Campbell (ANIC) (type not seen).

Material examined. Australia, Northern Territory, 1♂, South Alligator R. at Gimbat, 13°34'S, 132°37'E, 24 May 1988, light trap, A. Wells and P. Suter (♂ genitalic prep. PT–1816 figured) (NMV); 1♂, Litchfield National Park, Tolmer Falls, 13°12'S, 130°43'E, MV–light, 4 Sept 1992, A. Wells and J. Webber (NTMD).

North Queensland, Cape York: 1♂, Gunshot Creek — Telegraph x-ing, 11°44'S, 142°29'E, 14 Feb 1992, D. Cartwright and A. Wells (QM); 2♂, Bertie Creek, 1km SE Heathlands H.S., 11°34'S, 142°35'E, 4 Feb 1992, D. Cartwright and A. Wells (NMV); 3♂, Tributary of Bertie Creek 250m SW Heathlands H.S., 4 Feb 1992, D. Cartwright and A. Wells (QM); 1♂, 1♀, same locality 11 Feb 1992, D. Cartwright and A. Wells (NMV) (♀ genitalic prep. PT–1973 figured); 2♂, Eliot Creek above Canal Creek junction, 11°23'S, 142°25'E, 6 Feb 1992, D. Cartwright and A. Wells (QM); 2♂, Middle Claudie R., Iron Range, 12°46'S, 143°16'E, 2–9 Oct 1974, M. S. Moulds (NMV); 1♂, same locality 23 Oct 1974, M. S. Moulds (NMV); 1♂, 2♀, 6km ENE Mt Tozer, 12°44'S, 143°16'E, 30 Jun 1986, J. C. Cardale (ANIC; NMV); 4 ♂, 3km ENE Mt Tozer, 2 Jul 1986, J. C. Cardale (ANIC); 1 ♂, 9km ENE Mt Tozer, 5–10 Jul 1986, J. C. Cardale (ANIC); 1 ♂, Heathlands, 11°45'S, 142°35'E, 18 Aug 1992, at light, J. C. Cardale and P. Zborowski (ANIC).

Distribution. Originally described from a single male specimen from Northern Territory, Australia, it is now recorded from several localities on Cape York Peninsula.

Remarks. Males of this species (Figs 16, 17) are easily distinguished by the apically truncate superior appendanges, robust, apically pectinate inferior appendages, and strongly formed paraproctal processes. The phallus has a pair of curved spines. Female genitalia are as illustrated (Figs 18, 19), the sternite VIII with a distinct mesoventral keel, distal margin produced mesally into a distinct rounded lobe; and ventral plates rather elongate ovoid.

Paranyctiophylax gyratus sp. nov.

Figures 20–25

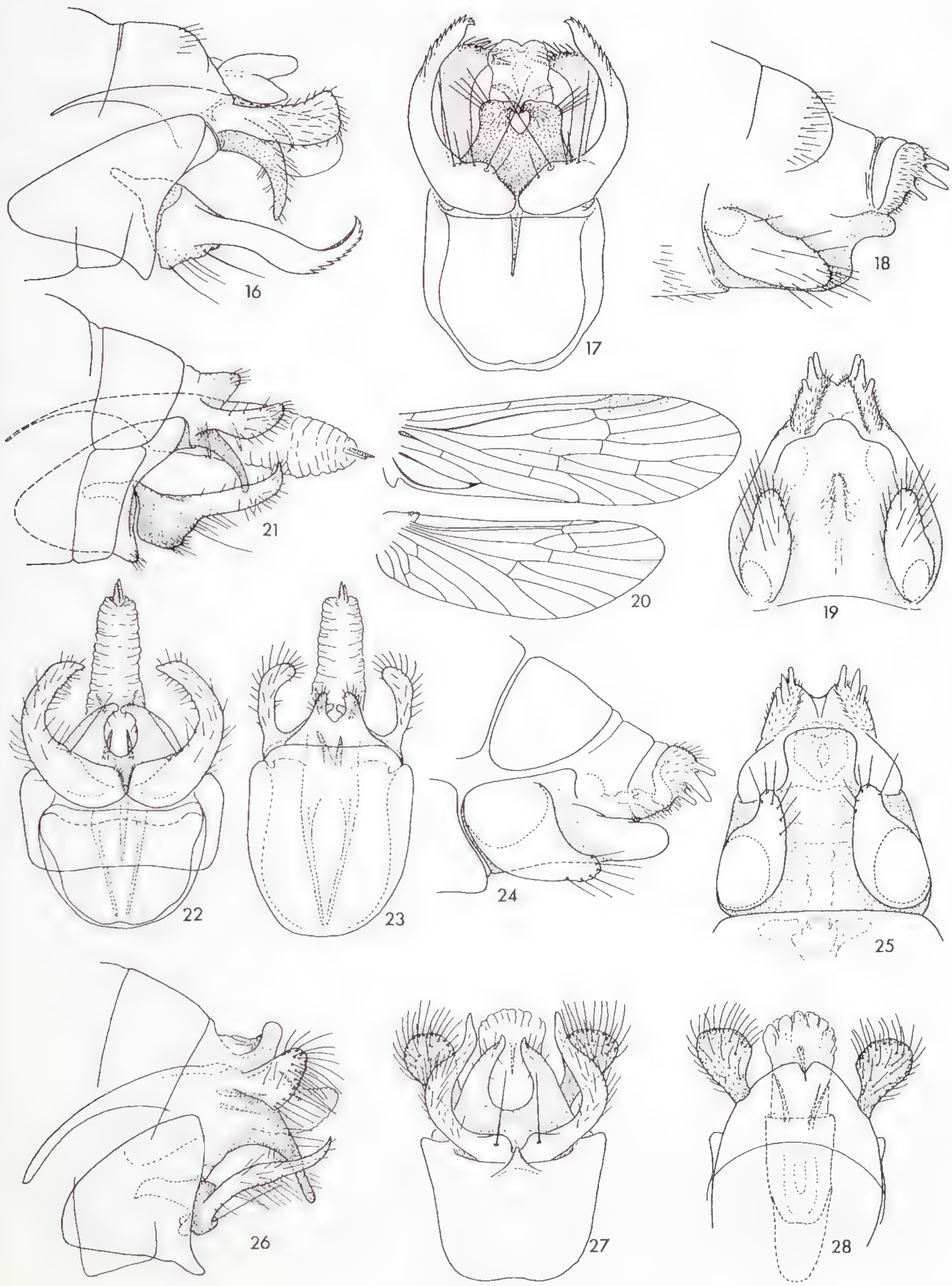
Type material. Holotype ♂, Papua New Guinea, Mamai Plantation, 10°16'S, 149°30'E, 150m asl., 6 Feb 1965, R. Straatman (BPBM) (♂ genitalic prep. PT–1785, specimen dry mounted). Paratypes: 1♂, 1♀, collected with holotype (BPBM); 2♀, same locality 27 Jan 1965, R. Straatman (BPBM, NMV) ♀ genitalic prep. PT–1965 figured, specimen in alcohol); 1♂ 2♀ same locality 29 Jan 1965, R. Straatman (BPBM, NMV) (♂ genitalic prep. PT–1952 figured, specimen in alcohol); 1♀, same locality 30 Jan 1965, R. Straatman (BPBM) (dry mounted).

Description. Colour of wings dark-greyish brown with obvious, somewhat triangular pale gray spot at base of median cell and small spot at arculus, venation as in Fig. 20. Length of fore wing: ♂ 3.6–3.7mm; ♀ 3.8–4.6mm.

Male genitalia (Figs 21–23) characteristic of genus; sternite IX subtriangular, mesoventral projection short; superior appendages elongate; paraproctal processes slightly wider at base, apices bluntly rounded; inferior appendages robust, broad at base, in ventral view evenly curved. Phallus with pair of apical chitinous spines and 2 pairs at base.

Female genitalia (Figs 24, 25) sternite VIII in ventral view broadly rectangular at apex, ventral plates broad at base, abruptly narrowed distally, apices rounded.

Distribution. South-eastern Papua New Guinea.



Figures 16–19, *Paranyctiophylax parvus*: 16, male genitalia lateral; 17, male genitalia ventral; 18, female genitalia lateral; 19, female genitalia ventral.
Figures 20–25, *P. gyratus*: 20, male wing venation; 21, male genitalia lateral; 22, male genitalia ventral; 23, male genitalia dorsal; 24, female genitalia lateral; 25, female genitalia ventral.
Figures 26–28, *P. flavus*: 26, male genitalia lateral; 27, male genitalia ventral; 28, male genitalia dorsal.

Etymology. From *gyrata* (Latin), 'turning around' in reference to the shape of the inferior appendages in ventral view.

Remarks. Males may be distinguished by the robust inferior appendages, and females by the broad rectangular sternite VIII.

Paranyctiophylax flavus (Ulmer, 1915)

Figures 26–28

Nyctiophylax flavus Ulmer, 1915: 45. — Ulmer, 1930: 424. — Ulmer, 1951: 122.
Paranyctiophylax flavus. — Neboiss, 1993: 108.

Material examined. 1♂, Papua New Guinea, Mamai Plantation, E of Port Glasgow, 10°16'S, 149°30'E, 150m asl, 27 Jan 1965, R. Straatman (NMV) (♂ genitalic prep. PT–1487 figured, specimen dry mounted).

Distribution. Papua New Guinea.

Remarks. The original material (1♂, 3♀) from the 'Kaiserin-Augusta-Fluss Expedition' (present day Sepik River, Papua New Guinea) was collected at the base camp, Malu village (04°15'S, 142°53'E) about 100m asl. None of this material has been located either at Berlin Museum, or in the Ulmer Collection, Hamburg. In the absence of type material and with insufficient details in the original illustrations, the species identity is somewhat uncertain. A specimen from Mamai Plantation, about 1000km south-east of the type locality, is here identified as this species, although with some reservation. The wing venation agrees with the described details, fore wing fork 4 and hind wing fork 2 are both sessile. Some details of male genitalia (Figs 26–28) appear slightly different, but this may be due to the original illustrations being prepared from a dried specimen. The tergite X (IX of Ulmer) is cleft apically, the superior appendages (appendages preanales of Ulmer) are proportionally smaller, the mesal spine (ein Dorn) is actually at the apex of the phallus and in dried specimen may protrude distally. Although three female specimens were collected within the original material, they are neither described nor figured. No new female specimens were available for study. The length of fore wing of males is 4.0–4.6mm.

The species is distinguished by the pale straw–yellow wing colour, the short and broad, rounded superior appendages and the mesal spine at the distal end of the phallus. The illustrations referred to *Paranyctiophylax flavus* by Neboiss 1993 represent *Paranyctiophylax gyratus* described in this paper.

Paranyctiophylax eidolonus sp. nov

Figures 29–33

Type material. Holotype ♂, Australia, North Queensland, Upper Freshwater Creek, Whitfield Range nr Cairns, 16°56'S, 145°42'E, 24 Aug 1974, M. S. Moulds (NMV, T–12296. Paratypes: 9♂, 4♀, collected with the holotype (NMV) (♂ genitalic prep. PT–1977 figured); 4♂, 2♀, same locality, 15 Dec 1974, M. S. Moulds (ANIC; NMV; QM); 4♂, same locality, 3 Apr 1975, M.S. Moulds (NMV); 40♂, 15♀, Mossman Gorge, Daintree National Park, 17 Nov 1988, K. Walker (♀ genitalic prep. PT–1996 figured) (BPBM; NMV; QM; RMNH); 5♂, Mulgrave River 8km NW of Gordonvale, 15 Nov 1988, K. Walker (NMV); 2♂, 2♀, Crystal Cascades nr Cairns, 10 Jun 1971, E. F. Rick (ANIC; NMV) (dry mounted).

Other material examined. North Queensland, 3♂, Gap Creek, Mt Finlayson Range, S of Cooktown, 23 Nov 1974, M. S. Moulds (NMV); 3♂, Woobadda R., 15°58'S, 145°22'E, 25 Aug 1992, at light, J. C. Cardale and P. Zborowski (ANIC); 6♂, Behana Gorge nr Cairns, 17°11'S, 145°50'E, 16 Nov 1982, T. Hinger (NMV).

Description. Colour of wings dark greyish-brown, in dry specimens fore wings with dark costal margin as well as several dark spots on cross-veins and at bases of forks, also dark spot at arculus and at junction of anal veins. Wing venation similar to *P. flavus*, fore wing median cell closed. Length of fore wing: ♂ 4.2–5.2mm; ♀ 4.9–5.5mm.

Male genitalia (Fig. 29) characteristic of genus, sternite IX subtriangular, mesoventral projection in lateral view distinct; superior appendages elongate, rounded apically; paraproctal processes gradually widened near base, apices rounded; inferior appendages slender, curved, pointed apically, basal elbow distinct with several strong setae at base. Phallus (Figs 30, 31) terminating

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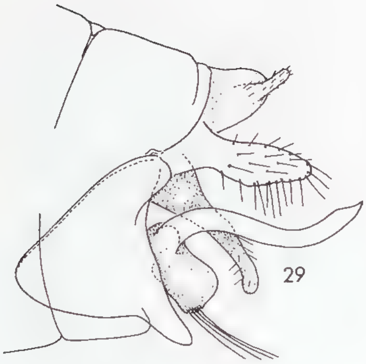
Figures 29–33, *Paranyctiophylax eidolonus*: 29, male genitalia lateral; 30, phallus lateral; 31, phallus ventral; 32, female genitalia lateral; 33, female genitalia ventral.
Figures 34–37, *P. dicellatus*: 34, male genitalia lateral; 35, apex of phallus lateral; 36, female genitalia lateral; 37, female genitalia ventral.
Figures 38–41, *P. basispinosus*: 38, male genitalia lateral; 39, apex of phallus lateral; 40, female genitalia lateral; 41, female genitalia ventral.



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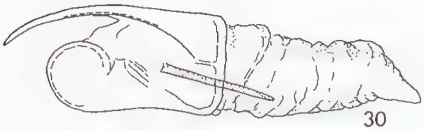

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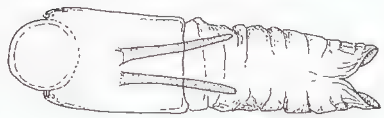

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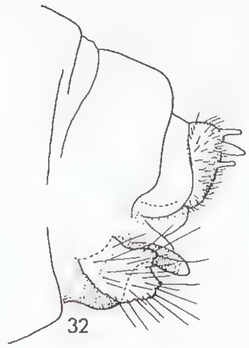

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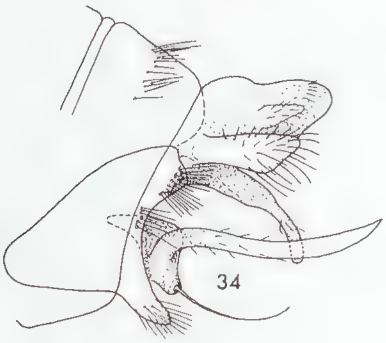

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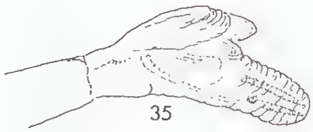

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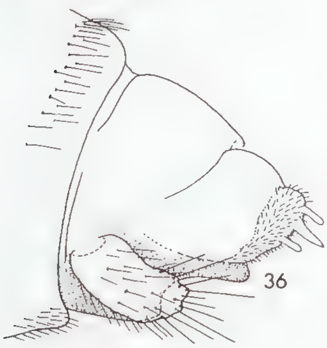

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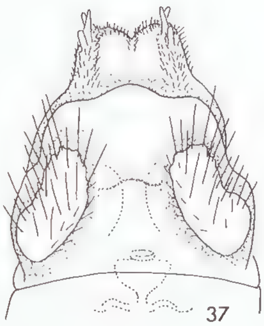

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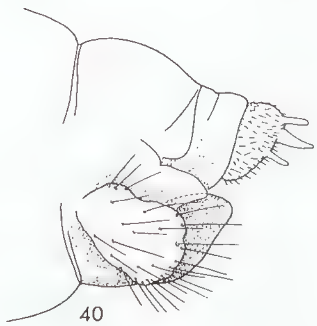

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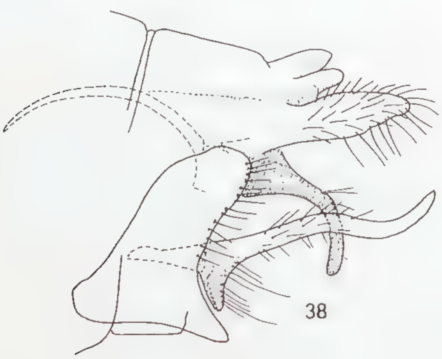

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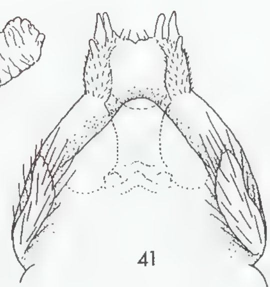

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in 2 triangular lobes apically, a pair of comparatively long chitinous rods near base.

Female genitalia (Figs 32, 33) sternite VIII short and broad, transversally concave, distal margin forming a downturned lip; ventral plates short, distal margin irregular.

Distribution. Australia, North Queensland.

Etymology. From *eidolon* (Greek), 'image', referring to the similarity with other species from northern Australia.

Remarks. Males can be readily distinguished by the strongly developed basal elbow of the inferior appendages and the distinct apex of phallus.

Paranyctiophylax dicellatus sp. nov.

Figures 34–37

Type material. Holotype ♂, Australia, North Queensland, Lock Creek, Davies Creek Rd, Lamb Range, Mareeba district, 16°59'S, 145°33'E, 25 Dec 1976, M. S. Moulds (NMV, T–10117). Paratypes: 3♂, collected with holotype (NMV); 1♂, Upper Freshwater Creek, Whitfield Range nr Cairns, 3 Apr 1975, M. S. Moulds (♂ genitalic prep. PT–1979 figured) (NMV); 1♂, Mulgrave R. W of Gordonvale, 29 Apr 1979, A. Wells (NMV); 1♂, Grass Tree Pocket Rd, Annan River, Cooktown area, 15°49'S, 145°14'E, 1 Jan 1981, G. Daniels (QM).

Other material examined. 1♂, Yuccabine Creek, Kirrama State Forest, 18°12'S, 145°45'E, 2 Jan 1985, R. Pearson (NMV).

Description. Colour dark greyish-brown, wing venation similar to *P. flavus*, fore wing median cell closed. Length of fore wing: ♂ 3.7–4.5 mm.

Male genitalia (Fig. 34) with distal margin of sternite IX in lateral view concave, mesoventral projection present; superior appendages obliquely truncate apically; paraproctal processes with basal half obviously thickened, apex rounded; inferior appendages gently curved, basal elbow with single strong bristle. Phallus (Fig. 35) apically with pair of dorsolateral expandable lobes and pair of internal chitinous spines.

Female (Figs 36, 37) from type locality provisionally referred to this species.

Distribution. Australia, North Queensland.

Etymology. From *dikella* (Greek), having two prongs, in reference to the pair of spines within the phallus.

Remarks. The species may be identified by the strong bristle at the base of the inferior appendages and the position of the chitinous spines within the phallus.

Paranyctiophylax basispinosus sp. nov.

Figures 38–41

Type material. Holotype ♂, Australia, North Queensland, Yuccabine Creek, Kirrama State Forest, 18°12'S, 145°45'E, 2 Jan 1982, R. Pearson (NMV, T–10123). Paratypes: 2♂, 1♀, collected with holotype (NMV); 1♀, same locality, 3 Feb 1985 (♀ genitalic prep. PT–1958 figured) (NMV); 1♂, same locality, Oct. 1984, R. Pearson (NMV); 2♂, 1♀, same locality, Dec 1985, R. Pearson (NMV); 2♂, 1♀, same locality, Mar 1986, R. Pearson (♂ genitalic prep. PT–1589 figured) (NMV; QM); 1♀, Yuccabine Creek, 18°13'S, 145°45'E, 1982 (NMV).

Description. Colour dark greyish-brown, wing venation similar to *P. flavus*, fore wing median cell closed. Length of fore wing: ♂ 4.7–5.3 mm; ♀ 5.4–6.2 mm.

Male genitalia (Fig. 38) with sternite IX short, dorsal margin in lateral view comparatively broad, mesoventral projection present; superior appendages elongate ovate; paraproctal processes in lateral view expanded near base, apices rounded; inferior appendages slender, elongate curved, basal elbow not very obvious. Phallus (Fig. 39) with group of basal, ventrally directed internal spines, apex membranous.

Female genitalia (Figs 40, 41) with sternite VIII ventrally convex, in ventral view broadly triangular; ventral plates broad, attached sublaterally.

Distribution. Australia, North Queensland.

Etymology. References to the position of the group of spines within the phallus.

Remarks. Males of this species are distinguished by the reduced basal elbow of the inferior appendages and the group of chitinous internal spines at the base of the phallus.

Paranyctiophylax rhamphodes sp. nov.

Figures 42–46

Type material. Holotype ♂, Australia, Northern Territory, South Alliagtor R. above BHP camp, MV–light, 25 May 1988, A. Wells and P. Suter (NMV, T–10766). Paratypes: 1 ♂, collected with holotype (♂ genitalic prep. PT–1948 figured) (NMV); 1♂, South Alligator R. below BHP camp, 25 May 1988, A. Wells and P. Suter (NMV); 1♂, South Alligator R. below Fisher Creek junction, 24 May 1988, A. Wells and P. Suter (NMV); 40♂, 7♀, Baroalba Springs, Kakadu National Park, 12°48'S, 132°49'E, 25 Apr 1991, A. Wells and J. Webber (♀ genitalic prep. PT–1960 figured) (BPBM; NMV; NTMD; RMNH).

Other material examined. 5♂, South Alligator R., UDP falls, 7 Sep 1979, J. Blyth (NMV); 2♂, Graveside Gorge, 18 Jul

1988, P. Dostine (NTMD); 1♀, Radon Springs, 12°45'S, 132°55'E, 14 Apr 1989, P. Suter and A. Wells (NTMD).

Description. Colour dark greyish-brown, fore wing median cell open, venation as in Fig. 44. Length of fore wing: ♂ 3.4–3.9 mm; ♀ 3.9–4.3 mm.

Male genitalia (Figs 42, 43) with abdominal sternite IX in lateral view higher than long, subtriangular; superior appendages small, elongate ovoid; paraproctal processes long, distinct, curved ventrad; inferior appendages long, slender, curved dorsad, with outward directed beak-like projection apically, basal margin with several strong bristles. Phallus membranous, with a single internal spine near apex, directed dorsally, and pair of spines near base.

Female genitalia (Figs 45, 46) with ventral plates in lateral view short and broad; sternite VIII subtriangular, elevated mesobasally.

Distribution. Australia, Northern Territory.

Etymology. From *rhamphos* (Greek), "curving beak", referring to the shape of the inferior appendages.

Remarks. This new species is distinguished from others by the presence of a beak-like apicolateral projection on each inferior appendage.

Paranyctiophylax spiculatus sp. nov.

Figures 47–50

Type material. Holotype ♂, Australia, Kimberleys, Mitchell Plateau, Mining Camp Creek, 14°50'S, 125°50'E, 30 Jan 1978, J. E. Bishop (NMV, T–12386). Paratypes: 10♂, 4♀, collected with holotype (♂ genitalic prep. PT–1995 and ♀ PT–1994 figured) (NMV; RMNH); 11♂, 1♀, same locality, 31 Jan 1978, J. E. Bishop (ANIC; NMV; QM); 1♂, same locality, 26 Feb 1978, J. E. Bishop (NMV); 5♂, same locality, 29 Feb 1978, J. E. Bishop (NMV); 1♂, same locality, 13 Jul 1978, P. Suter (NMV); 6♂, 3♀, Mitchell Plateau, Camp creek at crusher, 15 Feb 1979, J. E. Bishop (NMV).

Other material examined. Western Australia, Kimberleys, 1♂, Spillway Creek, 2 Feb 1978, J. E. Bishop (NMV); 1♂, 1♀, Ord River, 9 km N of Kunnanurra, 19 Sep 1979, J. Blyth (NMV); 2♂, Theda H.S., Morgan. 28 Sep 1979, J. Blyth (NMV); 1♂, Adcock Gorge, Gibb River–Derby Rd, 2 Oct 1979, J. Blyth (NMV); 2♂, 1♀, Drysdale R. at Kalumbura road crossing, 28 Sep 1979, J. Blyth (NMV); 1♂, 2♀, Granite Ck, Kunnanurra — Lake Argyle H-way, 2 Feb 1978, J. E. Bishop (NMV); 1♂, Fine Springs Ck, between Lake Argyle–Duncan H-way, 23 Feb 1977, J. E. Bishop (NMV); 2♂, 1♀, King Edward R., 4 May 1992, P. S. Cranston (ANIC, NMV); 9♂, 5♀, Barnett River Gorge, Barnett Station, 1 Oct 1979, J. Blyth (NMV).

Western Australia, Pilbara, 43♂, 13♀, Fortescue Falls, Hammersley Range National Park, 27 Oct 1979, J. Blyth (BPMB, NMV), 2♂, Fortescue R., Millstream S of Roebourne, 12 Nov 1978, M. S. and B. J. Moulds (NMV); 2♂, Crossing Pool, Millstream, 21 Oct 1979, J. Blyth (NMV); 27♂, 6♀, Fortescue R., Millstream National Park, 24 Apr 1992, P. S. Cranston (ANIC); 1♂, Millstream National Park, Deep Reach, 24 Apr 1992, P. S. Cranston (ANIC); 5♂, Lockyer Gorge, Harding River, 19 Oct 1979, J. Blyth (NMV); 3♂, 3♀, Wittenoom Gorge, 5 km S of Wittenoom, 26 Oct 1979, J. Blyth (NMV); 2♂, Wittenoom Gorge, Hammersley Range, 20 Feb 1977, M. S. Moulds (NMV).

Northern Territory, 1♂, 2♀, Howard Creek, 3 km E of Howard Springs, 17 Aug 1979, J. Blyth (NMV).

Description. Colour dark brown, similar in both sexes; wing venation similar to *P. flavus*, fore wing median cell closed. Length of fore wing: ♂ 3.2–4.0 mm; ♀ 3.9–4.4 mm.

Male genitalia (Figs 47, 48) similar to *P. rhamphodes*; sternite IX in lateral view distinctly triangular, distal margin with mesoventral projection; superior appendages elongate ovoid; paraproctal processes strongly curved ventrad, pointed apically; inferior appendages slender, curved, laterally somewhat flattened, base usually gradually widened to distinct elbow, widening sometimes may be rather abrupt, a small hook apically. Phallus with a group of chitinous spines apically.

Female genitalia (Figs 49, 50) with sternite VIII in lateral view transversely depressed, basal mesoventral part forming small, blunt keel.

Distribution. Australia, Kimberley and Pilbara regions of Western Australia.

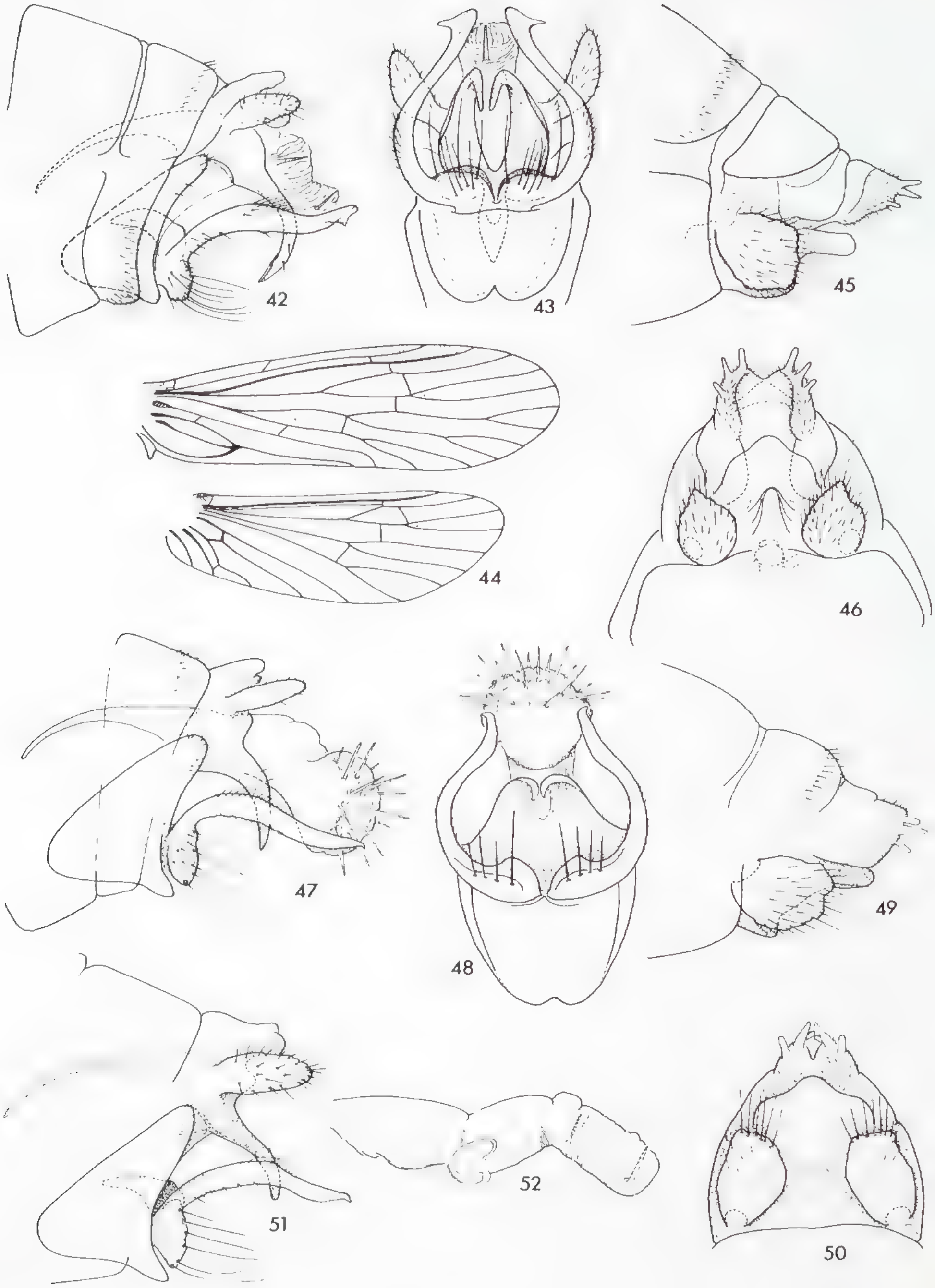
Etymology. From *spica* (Latin), 'spine', in reference to the spines on the phallus.

Remarks. The species is similar to *P. rhamphodes* but may be distinguished by the small apical hook on the inferior appendages and the clavate apex of the phallus with chitinous spines. The specimens from the Pilbara region of Western Australia show minor differences in both male and female genitalia. In males the paraproctal processes are rounded apically and the spines on the phallus are less numerous; in females the meso-ventral keel is less angular.

Paranyctiophylax apicatus sp. nov.

Figures 51, 52

Type material. Holotype ♂, Australia, Cape York Peninsula, Middle Claudie R., Iron Range, 12°46'S, 143°16'E, 2–9 Oct 1974, M. S. Moulds (NMV, T–10134). Paratypes: 1♂, collected with holotype (NMV); 2♂, same locality, 23 Oct, 1974, M. S. Moulds (♂ genitalic prep. PT–1970 figured) (NMV); 2♂, Claudie River 25 km NW of Lockhart River, 12°44'S, 143°16'E, 10 Nov 1988, K. Walker (NMV); 2♂,



Figures 42–46, *Paranyctiophylax rhamphodes*: 42,male genitalia lateral; 43,male genitalia ventral; 44,male wing venation; 45, female genitalia lateral; 46, female genitalia ventral.
Figures 47–50, *P. spiculatus*: 47,male genitalia lateral; 48,male genitalia ventral; 49, female genitalia lateral; 50, female genitalia ventral.
Figures 51, 52, *P. apicatus*: 51,male genitalia lateral; 52, apex of phallus lateral.

Dulhunty R. Telegraph crossing, 11°50'S, 142°30'E, 10 Feb 1992, D. Cartwright and A. Wells (QM); 1♂, Tributary of Bertie Ck, 250m SW Heathlands H.S., 11°45'S, 142°35'E, 11 Feb 1992, D. Cartwright and A. Wells (QM); 2♂, Cockatoo Ck Telegraph crossing, 11°39'S, 142°27'E, 5–6 Feb 1992, D. Cartwright and A. Wells (NMV, QM); 1♂, Wenlock River Telegraph crossing, 12°28'S, 142°38'E, 15 Feb 1992, G. Byron and D. Blake (NMV); 4♂, Canal Ck above Eliot Ck junction, 11°23'S, 142°25'E, D. Cartwright and A. Wells (QM, RMNH); 2♂, Gunshot Ck Telegraph crossing, 10–11 Apr 1992, M. Crossland (ANIC).

Other material examined. Australia, Northern Territory, 2♂, South Alligator R. at Gimbat OSS station, 24 Mar 1988, MV–light, A. Wells and P. Suter (NMV, NTMD); 1♂, Groote Eylandt, Amagule Pool, 6 Feb 1984, M. Davies (NMV).

Description. The size and colour similar to other species found in Northern Australia; fore wings with median cell closed. Length of fore wing: ♂ 3.2–3.9 mm.

Male genitalia (Fig. 51) sternite IX in lateral view subtriangular, mesoventral projection present; superior appendages elongate ovoid; paraproctal processes bluntly rounded apically; inferior appendages with small apical hook, basal elbow with several strong bristles. Phallus (Fig. 52) with a single apical spine and a pair of basal spines.

Female not positively associated.

Distribution. Australia, Cape York Peninsula, Northern Territory.

Etymology. Reference to the arrangement of spines inside the phallic apex.

Remarks. This species most closely resembles *P. spiculatus*, differing primarily by the single apical spine of the phallus.

Paranyctiophylax traunensis sp. nov.

Figures 53–57

Type material. Holotype ♂, Papua New Guinea, Baiyer River Sanctuary, Trauna River, 05°35'S, 144°10'E, UV–light, 17 Jun 1986, A. Wells (NMV, T–10744) (♂ genitalic prep. PT–1788 figured). Paratypes: 1♀, Baiyer River, 1150m, 19 Oct 1958, J. L. Gressitt (NMV) (♀ genitalic prep. PT–1953 figured); 2♂, Tifalmin, 1360 m, 19 Aug 1963, R. Straatman (BPBM); 2♂, same locality, 21 Aug 1963, R. Straatman (BPBM); 1♂, same locality, 1400m, 20 Aug 1963, R. Straatman (BPBM); 1♂, Feramin, 1450m 27 Aug 1963, R. Straatman (NMV); 4♂, Mamai Plantation, E of Port Glasgow, 10°16'S, 149°30'E, 150m, 5 Feb 1965, R. Straatman (BPBM, NMV) (All paratypes are dry mounted).

Description. Colour yellowish-brown; fore wing median cell open, hind wing fork 2 with short footstalk, venation as in Fig. 55. Length of fore wing: ♂ 5.4–5.9 mm; ♀ 5.5 mm.

Male genitalia (Figs 53, 54) with abdominal sternite IX about as long as high, subtriangular, ventral margin produced, broadly rounded; superior appendages in lateral view elongate ovoid, inner margin with large angular lobe; paraproctal processes moderately long, straight, apices obliquely rounded, slightly widened; inferior appendages slender, curved dorsad, basal elbow distinct. Phallus membranous with 2 pairs of internal sclerotised spines.

Female genitalia (Figs 56, 57) sternite VIII forming broad, slightly sclerotised lip.

Distribution. Papua New Guinea.

Etymology. Reference to the type locality.

Remarks. The species may be separated from others by the mesal angular lobe on the superior appendages and the straight paraproctal processes.

Paranyctiophylax synorius sp. nov.

Figures 58–62

Type material. Holotype ♂, Bougainville I., Panguna, 06°10'S, 155°30'E, 7 Dec 1989, C. Yule (NMV, T–10786). Paratypes: 2♀, collected with holotype (♀ genitalic prep. PT–1954 figured); 2♂, same locality, 19 Dec 1989, C. Yule (♂ genitalic prep. PT–1827 figured); 2♀, same locality, 29 Jan 1989, C. Yule (NMV).

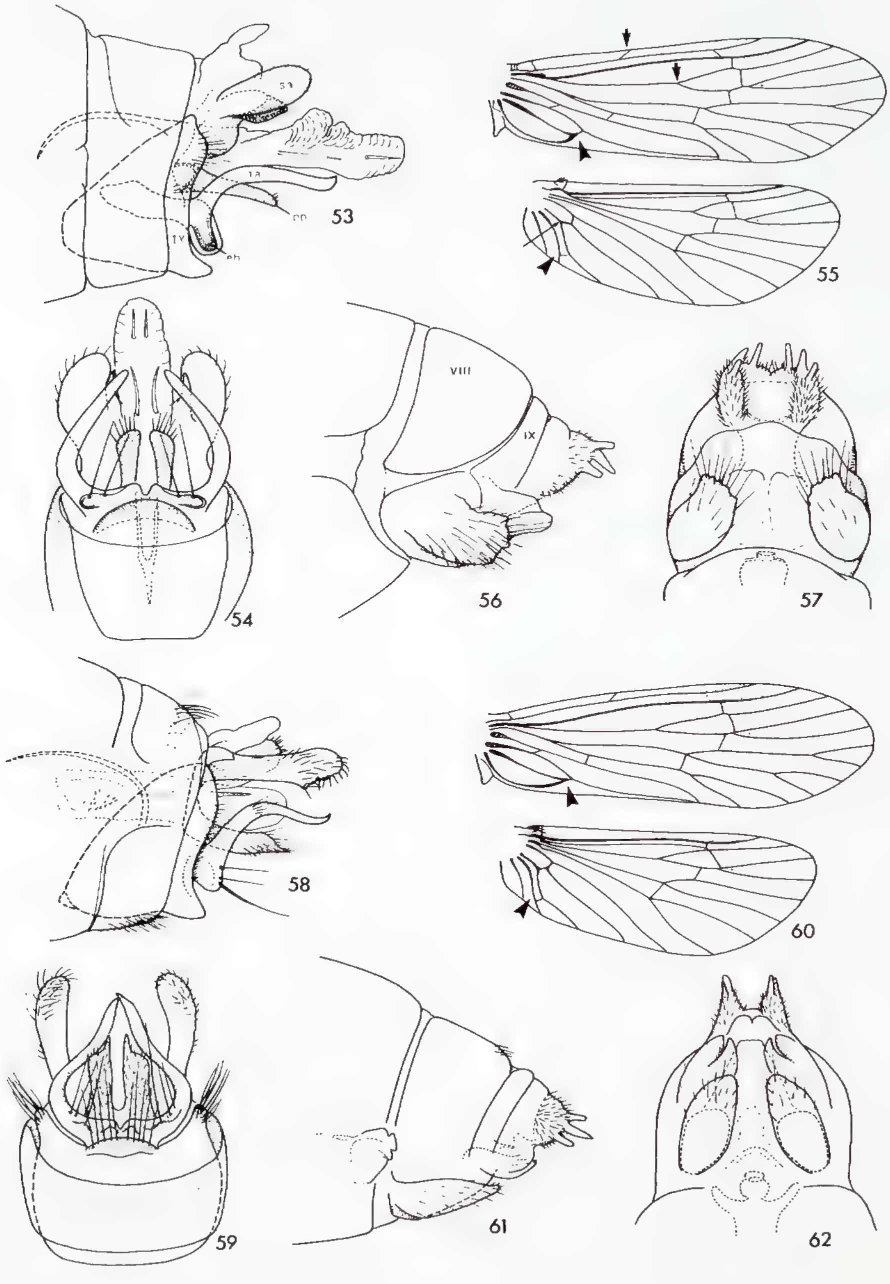
Description. Dark greyish-brown, fore wings with median cell open, venation as in Fig. 60. Length of fore wing: ♂ 5.2–5.4 mm; ♀ 5.9–6.2 mm.

Male genitalia (Figs 58, 59) abdominal sternite IX in lateral view robust, distomesal margin forming slightly produced lip; superior appendages straight, slightly clavate; paraproctal processes slightly curved dorsally, mesodistal angle acutely produced, directed posteriorly; inferior appendages slender, strongly curved, each with strong dark bristle at the base of elbow. Phallus with pair of sclerotized spines apically and a group of small spinules on phallobase.

Female genitalia (Figs 61, 62) with ventral plates elongate ovoid, rather close ventrally; sternite VIII with mesal lip truncate, flanked by 'tusk-like' lobes.

Distribution. Bougainville Island.

Etymology From *synoria* (Greek), 'borderland' in reference to the most easterly location.



Figures 53–57, *Paranyctiophylax traunensis*: 53,male genitalia lateral; 54,male genitalia ventral; 55,male wing venation; 56, female genitalia lateral; 57, female genitalia ventral.
Figures 58–62, *P. synorius*: 58,male genitalia lateral; 59,male genitalia ventral; 60,male wing venation; 61, female genitalia lateral; 62, female genitalia ventral.

Remarks. The species is distinguished from other species by the distinct paraproctal processes and a group of spinules on the phallobase.

Acknowledgements

I wish to thank Dr J. Van Tol, Leiden for providing access to specimens from Sulawesi; Dr K. Tanida, Osaka and Dr V. Ivanov, St Petersburg for providing specimens of *P. kisoensis* and the types of *P. digitatus* respectively; to Mr G. Nishida, Honolulu for sending specimens collected in New Guinea, Ms C. Yule, Melbourne for donation of specimens from Bougainville I., and to Dr A. Wells, Mr J. Dean and Mr K. Walker for comments on the manuscript.

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REVISION OF THE GENUS *PLATYCOLASPIS* JACOBY (COLEOPTERA: CHRYSOMELIDAE: CRYPTOCEPHALINAE)

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Abstract

Reid, C. A. M., 1994. Revision of the genus *Platycolaspis* Jacoby (Coleoptera: Chrysomelidae: Cryptocephalinae). *Memoirs of the Museum of Victoria* 54: 207—220.

The genus *Platycolaspis* Jacoby, hitherto placed in Eumolpinae, is redescribed in the Cryptocephalinae. This south-east Australian genus includes five species, four of which are new: *P. alpina* sp. nov., *P. australis* Jacoby, *P. lamingtonensis* sp. nov., *P. mcquillani* sp. nov. and *P. pubescens* sp. nov. The genus has affinities with *Semelvillea* Reid. Adults of *Platycolaspis* species feed on flowers of *Acacia* or on *Nothofagus* foliage.

Introduction

The genus *Platycolaspis* Jacoby was originally tentatively placed in the Colaspini, Eumolpinae, where it has remained (Seeno and Wilcox, 1982). It was described from specimens sent for identification by Lea. However other material of *Platycolaspis* seen by Lea (Museum of Victoria and South Australian Museum) includes specimens labelled by him 'allied to *Cryptocephalus pauperculus*' and 'note abdominal fovea' and it seems that Lea was aware of its affinities to the Cryptocephalinae. For placement in Cryptocephalinae, the structures of the female, the male genitalia and the case-bearing larva (not described here) are decisive.

The genus *Platycolaspis* is redescribed below and compared with other genera in the Cryptocephalinae, especially *Semelvillea* Reid. The five species are described. The relative abundance of material of four species is partly due to recent ecological surveys in Tasmania and Lamington National Park.

Methods. Dissections were made from dried material after separating the abdomen in water, soaking this in cold dilute KOH for 2–3 hr and then washing in water. The general morphology of Cryptocephalinae is typical of Chrysomelidae, but there are a few internal abdominal structures peculiar to Cryptocephalinae, which appear useful for generic or species discriminations. The male has an ejaculatory guide (Karren, 1966) for the flagellum in the median lobe of the aedeagus, which is greatly reduced in *Platycolaspis* but visible through the thin walls of the median lobe. The ovipositor is abruptly foreshortened and valvifer, coxite and stylus are fused into a single blade-like and partially transparent vaginal palp (Erber, 1968), which may show specific differences. The female rectum shows slight differences between species but is relatively invariable at generic level. It is differentiated into dorsal and ventral halves with areas of sclerotisation on the external surface (sclerites) and sensilla and rows of teeth (forming chitinpolsters) on the inner surface. The nomenclature used here for these structures was devised by Erber (1968). The generic redescription given here includes details of head and thoracic anatomy based on dissections of *P. australis* Jacoby, *P. mcquillani* sp. nov. and *P. pubescens* sp. nov.

Plants were identified by reference to Costermans (1981).

The material used in this study is deposited at the following institutions: Australian National Insect Collection, Canberra (ANIC); Natural History Museum, London (BMNH); Bernice P. Bishop Museum, Hawaii (BPBM); Griffith University Insect Collection (GUIC); Museum of Victoria, Melbourne (NMV); South Australian Museum, Adelaide (SAM); Insect Collection, Agriculture Department of Tasmania, Hobart (TAIC); University of Queensland Insect Collection, Brisbane (UQIC).

Platycolaspis Jacoby

Platycolaspis Jacoby, 1908: 27. (in Eumolpinae; type species: *Platycolaspis australis* Jacoby, by monotypy). — Clavareau 1914: 34. — Seeno and Wilcox, 1982: 58.

Diagnosis. Cryptocephalinae (sensu stricto) of 1.4–3.0mm; antennal segments with basiconic sensilla scattered, not concentrated in apical discs; eye evenly and strongly convex, canthus not developed (Fig. 4); pronotal disc with median transverse impression, at least at sides,

and hind margin without teeth (Figs 1–3); procoxal cavities open or closed by prosternal process touching or slightly overlapping hypomeron (Figs 11–13); scutellum abruptly declined anteriorly (Figs 1–3); elytral interlocking grooves evanescent and recurved before apex; abdomen covered by elytra, at least in males; claws appendiculate (Fig. 19); tergites weakly sclerotised, soft and flexible; male with sternites V and VI fused; median lobe of aedeagus with simple apex (Figs 20, 22–27); ejaculatory guide simple, elongate–conical; spermatheca with elongate collum (Figs 33–39); kotpresse with ventral sclerite laterally extended (Figs 40–44).

Description. Habitus (Figs 1–3). Size 1.4–3.0 mm; body moderately cylindrical but head, prothorax and hindbody distinguishable; colour of dorsum various shades of yellowish- or reddish-brown, venter similar but may be partly black; without metallic reflection; dorsum glabrous or pubescent.

Head (Fig. 4): relatively broad because of convex eyes, projecting from prothorax; vertical punctation dense, tending to rugose–strigose, interspaces c.1 puncture diameter or less; eyes evenly convex, relatively small, distance between always greater than 1.5 times eye length; inner margin of eye without canthus, straight or feebly concave; sides of clypeus divergent to apex; antennae (Fig. 7) with all segments elongate, 5–11 approximately equally long, 7–11 expanded; antennal length 0.4–0.6 body length; antennal segments with basiconic sensilla scattered, not in apical pits; labrum (Fig. 8) quadrate, with 3 or more pairs of dorsal setae and less than 10 pairs of basiconic sensilla on epipharynx; last segment of maxillary palpi simply conical to expanded at apex, with 3–4 digitiform sensilla; mandible with 2 short apical teeth, a blunt median tooth on internal edge and several short external setae; apical segment of labial palp shaped as maxillary palp.

Thorax: Prothorax (Figs 1–3, 5, 9–13): pronotum broadest at middle of sides, which are rounded to strongly angulate and only slightly contracted at apex; lateral margins of pronotum strongly bordered to explanate; disc strongly and closely punctured, with median transverse depression at least at sides; anterior corner setae set on anterior margin not on explanate border, posterior setae at corners; prosternal process quadrate to elongate, narrowed in middle (width less than 0.5 coxal cavity width) and expanded at apex; procoxal cavity narrowly open (gap between hypomeron and prosternal process less than length of hypomeral lobe), or closed by overlap or touching of prosternal process on hypomeron; scutellum abruptly elevated from mesoscutum, elongate with slightly broader base than truncate apex, or equilateral–triangular with rounded apex; mesoscutum with neither lateral patches of microchaetae, a longitudinal median ridge nor a broad stridulatory file; elytra (Figs 1–3, 9–10, 14–15) 2.5–3.0 times length of pronotum, subparallel-sided for basal half; apex of elytral sutural locking mechanism evanescent before apex, the dorsal ridge recurved on the elytra; punctation of elytra confused or subseriate on disc; epipleuron gradually attenuate, not reaching apex, with a row of punctures; mesosternal process narrow and truncate; wing venation reduced (Fig. 16), basal marginal vein of R-cell absent or incomplete and anal area with faint indication of elongate basal cell, oval apical cell and 2 radiating veins, outermost free; metasternum not convexly swollen ventrally, sides strongly punctured, dull, disc sparsely and weakly punctured, shining; metendosternite (Fig. 17) with basal stalk narrow, as long as lateral arms, without strong median projection and without lateral lobes or lamellae; all femora of similar size, thin, without ventral keel; tibiae unkeeled and apical spurs absent; all tarsal segments (Fig. 18) relatively short and dorsally convex, segment 3 of anterior tarsus slightly transverse; claws appendiculate (Fig. 19).

Abdomen (external) (Fig. 6): tergites thin, weakly sclerotised and not reaching sternites; pleurites absent, spiracles free in basal tergites; sternites weakly and sparsely punctured, relatively shining, but transversely microsculptured; sides of sternite III ridged at base of lateral lobe, ridge 0.5–0.75 length of sternite, other sternites unridged; male sternites V and VI connate, but sternite VII not indented; females with sternites V and VI free and sternite VII with large shallow egg-hollow lacking apical indentation.

Male genitalia (Figs 20–27): median lobe shallowly curved in profile, with generally short and sparse dorsal and ventral setae; ejaculatory guide reduced to a narrow cone with central channel and basal diaphanous vesicle (difficult to distinguish); tegmen (Fig. 21) U- or V-shaped with expanded sides and truncate base.

Female genitalia and oviposition complex (Figs 28–45): vaginal palp (Figs 28–32) with apical border wholly sclerotised and rounded to slightly concave; spermatheca (Figs 33–39) with

moderately long collum and U- or slightly V-shaped receptaculum; kotpresse (Figs 40–45) with laterally expanded ventral sclerite, conspicuous and usually triangular dorsal sclerites reaching lateral margins, and no subsidiary median sclerites; dorsal anterior and posterior surfaces of rectum with weakly spined sensilla, venter without sensilla except the narrow apical band. Microsculpture consisting of short sharp triangular spines on dorsal chitinpolster, and of multispined scales on ventral chitinpolster.

Distribution and biology. The species are found in south-east Australia (Fig. 46) from Tasmania north along the Dividing Range and coastal plains to Lamington National Park, southern Queensland, and west to Mount Gambier, South Australia. They may be locally abundant but seem to have restricted adult activity periods. Host plants are recorded for two species: *P. australis* feeds on the flowers of a wide range of *Acacia* species, and *P. mcquillani* feeds on the immature leaves of *Nothofagus* species. As is typical for Cryptocephalinae (Erber, 1988), eggs are dropped to the ground in scatoshells.

Remarks. *Platycolaspis* shows typical adult morphological attributes of Cryptocephalinae (sensu Lawrence and Britton, 1991) and the life history, with egg and larva in a scatoshell, supports this. Within the Cryptocephalinae, it shows affinity with a small group of little-known Australasian genera, including *Arnomus* Sharp, *Atenesus* Weise, *Leasia* Jacoby, and *Semelvillea* Reid (Reid, 1991).

Platycolaspis is similar to *Semelvillea*, with which it shares the following features: sutural locking mechanism evanescent before apex; male sternites V and VI connate; sides of sternite III partially ridged. It differs by: canthus absent; mid-antennal segments not obviously longer or wider than apical segments; front edge of pronotum not ridged; R-cell of wing open; third protarsal segment transverse and tarsi generally shorter and more convex; ejaculatory guide reduced to a simple conical structure; ventral rectal sclerite laterally expanded.

Key to species of *Platycolaspis*

1. Lateral margin of pronotum sharply angulate in middle and broadly explanate (Fig. 1); dorsum glabrous 2

— Lateral margin of pronotum weakly angulate or rounded, and narrowly margined (Figs 2–3); dorsum glabrous or pubescent.......... 3

2. Size, ♂ 1.4–1.5 mm, ♀ 1.6–1.7 mm; elytra, c. 2.5 times length of pronotum (Fig. 10); front angles of pronotum anteriorly produced; procoxal cavities closed, by overlap of prosternal process on hypomeron .... *P. lamingtonensis*

— Size, ♂ 1.7–2.3 mm, ♀ 2.3–2.7 mm; elytra, c. 3 times length of pronotum (Fig. 9); front angles of pronotum not anteriorly produced; procoxal cavities open .... *P. australis*

3. Dorsum apparently glabrous (minute setae present) (Fig. 2) .... *P. mcquillani*

— At least pronotum conspicuously pubescent (Fig. 3) 4

4. Pronotum with continuous transverse impression just posterior to middle and elytral apex abruptly angled in profile (Figs 3, 15); head and pronotum rugosely punctured, with ridged interspaces; elytral setae long, erect or recurved; frontoclypeus dull, microreticulate ....*P. pubescens*

— Pronotum slightly depressed either side of middle and elytral apex more evenly curved (Fig. 14); punctures of head and pronotum distinct, interspaces flat; elytral setae short, recurved; frontoclypeus shining, not microreticulate .... *P. alpina*

Platycolaspis alpina sp. nov.

Figures 14, 28, 33, 40

Type. Holotype ♀: / Bogong Plains VIC 5000–6000ft January 1928 F. E. Wilson / Id. by A. M. Lea *Cryptocephalus rufescens* Boh (*pauperculus* Germ.) ♂ is black / F. E. Wilson Collection / [NMV T–12501].

Diagnosis. Head and pronotum with small but conspicuous punctures, interspaces flat; pubescence on head and pronotum dense and conspicuous, on elytra short, recurved and much less conspicuous; pronotum convex, with shallow lateral median depressions; pronotum and apex of elytra evenly curved in profile.

Description (female only). Colour: yellowish-brown, with head and tarsi slightly darker and antennomeres 6–11 dark brown. Pubescence: head with short inconspicuous setae on disc, pronotum with conspicuous but adpressed curved setae arising from punctures; elytra with setae similar to pronotum but punctures much larger and sparser, therefore setae less visible; venter clearly pubescent. Size: 2.1 mm.

Head and pronotum relatively finely punctured, punctures close but separated by flat interspaces which are strongly microreticulate; eyes small but convex, interocular space about 3 times eye length; frontoclypeus shining, not microsculptured; antenna half body length, segments 7–11 slightly expanded towards apex; last segment of maxillary palp elongate–conical; explanate lateral margins of pronotum narrow, evenly rounded and tapering posteriorly; pronotum with transverse median depression shallow and separated by convex pronotal disc (Fig. 14); fore coxal cavities narrowly open, gap much less than half length of hypomeral lobe; prosternal process almost quadrate, medial width almost equal to coxal cavity length; apex of process curved.

Elytra: strongly and closely punctured, diameter of punctures more than twice pronotal punctures, confused, without longitudinal ridged intervals; epipleura at about 45° to vertical; apex of elytra evenly curved in profile (Fig. 14); scutellum equilateral–triangular with rounded apex;

Female: vaginal palp elongate–ovate (Fig. 28); spermatheca U-shaped (Fig. 33), with evenly rounded tip and relatively short straight collum; kotpresse (Fig. 40) with dorsal transverse sclerites only weakly projecting, subtriangular, ventral transverse sclerite broad, parallel-sided and projecting, but not expanded or crenulate.

Distribution and biology. Known only from the type locality in the Victorian Alps, where it was collected in January.

Platycolaspis australis Jacoby

Figures 1, 4–6, 9, 11, 19–21, 29, 34, 41

Platycolaspis australis Jacoby, 1908: 27. — Clavareau, 1914: 177. — Lea, 1915: 102, 110.

Types. Lectotype ♂, here designated: /Type H. T./ Hobart Tas: Lea/ Lea 10336/ Jacoby Coll. 1909–28a/ Platycolaspis australis Jac. type/ [BMNH].

Paralectotypes (3 specimens), here designated: 2♂ 1♀ /Hobart, Tasmania/ Jacoby Coll. 1909–28a/ [BMNH].

Other material (70 specimens). Tasmania. Hobart (BMNH, SAM), Launceston (SAM), National Park (SAM).

Victoria. Belgrave (NMV), Cheltenham (NMV), 5 km S Colquhoun (ANIC), Emerald (SAM), Lakes Entrance (ANIC), Point Ricardo (ANIC), Sandringham (ANIC), Somerville (MVM), 3 km S Weeragua (ANIC).

New South Wales. 15 km NE Batemans Bay (ANIC), Bundanoon (ANIC), 11 km E Marulan (ANIC).

Australian Capital Territory: Black Mountain (ANIC), Bulls Head (ANIC), 3 km E Piccadilly Circus (ANIC), Tidbinbilla NR (ANIC).

Diagnosis. Size, ♂ 1.7–2.3 mm, ♀ 2.3–2.7 mm; upper surface glabrous; lateral margins of pronotum strongly expanded and angulate; procoxal cavities open; length of elytra c. 3 times pronotal length; humeral elytral keel present but not sharply carinate.

Description. Colour: male with head, most of ventral surface, tarsi, femora and antennomeres 6 or 7–11 brown, rest pale brownish-yellow; female usually entirely pale brownish-yellow with darker antennae, but may be slightly darker in same areas as male, although not as dark. Pubescence: dorsum glabrous, venter with only abdomen conspicuously pubescent. Size: male 1.7–2.3 mm, female 2.3–2.7 mm.

Head and pronotum densely punctured and microsculptured, punctures deep and separated by narrow ridges; eyes convex (Fig. 1), interocular space about 2.2–2.5 times eye length; frontoclypeus dull, strongly microsculptured; antenna half body length, segments 7–11 expanded but parallel-sided towards apex and elongate; last segment of ♂ maxillary palp broadly expanded to apex, ♀ parallel–sided; explanate lateral margins of pronotum (Figs 1, 9) broad and sharply angled in middle, front angles not anteriorly produced; pronotum with continuous transverse median depression; fore coxal cavities (Fig. 5, 11) clearly open, but gap less than half length of hypomeral lobe; prosternal process elongate and narrow, medial width much less than half coxal

cavity length; apex of process curved and slightly produced.

Elytra (Figs 1, 9): elongate, length c. 3 times pronotum; strongly and closely punctured, densely and finely around scutellum with interspaces only weakly convex, subseriate on disc; raised interstice from shoulder to apex prominent, but evenly convex, not sharply ridged; epipleura almost horizontal; apex of elytra abruptly sloped in profile; scutellum elongate, length > 1.3 times width.

Male: median lobe (Fig. 20) narrow and ventral and dorsal surfaces evenly curved in profile; apex broadly but weakly mucronate, with four long dorsal setae, approximately 0.25 width of median lobe, and scattered shorter setae.

Female: vaginal palp (Fig. 29) rhomboid with rather pointed tip; spermatheca (Fig. 34) U-shaped with a pointed tip and elongate collum; kotpresse (Fig. 41) with dorsal transverse sclerites subtriangular but extended and crenulately expanded, laterally, ventral transverse sclerite lengthened medially and strongly extended and crenulately expanded, laterally.

Distribution and biology. Platycolaspis australis is widespread from the tablelands and adjacent coast near Goulburn, to Melbourne and eastern Tasmania. Adults are present from August to October and feed on *Acacia* flowers. The following hosts have been recorded: *A. baileyana* Muell., *A. dealbata* Link, *A. longifolia* (Andr.) Willd., *A. mucronata* Willd. ex Wendl., *A. obtusata* Sieb. ex DC., *A. pycnantha* Benth., *A. terminalis* (Salisb.) Macbr. This list includes bipinnate and phyllodinous species, and it seems likely that any *Acacia* flowering from August to October will be a suitable host. The adult beetles burrow into individual flower heads and their yellowish colouration appears to be suitably cryptic for this purpose.

Remarks. Jacoby (1908) did not specify the number of specimens he examined, but more than one specimen is indicated from the species description. The male specimen from Hobart in BMNH with Jacoby's 'type' label is hereby designated lectotype. The three remaining specimens from Hobart in Jacoby's collection are designated paralectotypes.

Platycolaspis lamingtonensis sp. nov.

Figures 10, 24, 30, 35, 42

Types. Holotype: ♂ / Lamington NP QLD, O'Reilly's, 28°.14'S 153°.00'E, pyrethrum fogging rainforest, Dec 1991, DR [*Dysoxylum rufum*] 55, R. L. Kitching/ (ANIC).

Paratypes (7 specimens): 3♂, 3♀, same data as holotype except code nos DR51, DR3.6, SG [*Synoum glandulosum*] 3, SG6 (ANIC, GUIC); 1♂, as above except 4.Dec.1991, DR4 (ANIC).

Diagnosis. Size, ♂ 1.4–1.5 mm, ♀ 1.6–1.7 mm; upper surface glabrous; lateral margins of pronotum strongly expanded and angulate; procoxal cavities closed; length of elytra c. 2.5 times pronotal length; humeral elytral keel sharply carinate.

Description. Colour: male with abdomen, tibiae, tarsi, and antennomeres 7–11 dark brown to black, rest yellowish- or reddish-brown, head generally somewhat darker; female entirely yellowish-brown, head may be slightly darker. Pubescence: dorsum glabrous, venter with only abdomen conspicuously pubescent. Size: male 1.4–1.5 mm, female 1.6–1.7 mm.

Head and pronotum densely punctured and microsculptured, punctures deep and separated by narrow ridges; eyes convex, interocular space about 2.3–2.5 times eye length; frontoclypeus weakly shining but microsculptured; antenna about 0.4 body length, segments 7–11 expanded towards apex and slightly elongate; last segment of maxillary palp broadly expanded to apex in ♂, parallel-sided in ♀; explanate lateral margins of pronotum (Fig. 10) broad and sharply angled in middle, very narrow behind this, front angles strongly anteriorly produced; pronotum more convex than in *P. australis*, with continuous transverse median depression; fore coxal cavities closed; prosternal process elongate and narrow, medial width less than half coxal cavity length; apex of process curved.

Elytra (Fig. 10): short, length c. 2.5 times pronotum; strongly and closely punctured, densely and finely around scutellum with interspaces strongly convex, subseriate on disc; raised interstice from shoulder to apex prominent and sharply ridged; epipleura almost horizontal; apex of elytra abruptly sloped in profile; scutellum slightly elongate to quadrate, length < 1.3 times width.

Male: median lobe (Fig. 24) narrow and ventral and dorsal surfaces almost evenly curved in profile; apex right-angled with blunt tip, with four long dorsal setae, approximately 0.25 width of median lobe, and scattered shorter setae.

Female: vaginal palp (Fig. 30) ovate–rhomboid with rounded tip; spermatheca (Fig. 35) asymmetrically U-shaped with a pointed tip and elongate collum; kotpresse (Fig. 42) with dorsal transverse sclerites transverse, feebly extended and

not crenulately expanded, ventral transverse sclerite parallel-sided, laterally extended but not crenulately expanded.

Distribution and biology. Platycolaspis lamingtonensis is confined to the type locality, Lamington National Park, 800 km north of any other species of *Platycolaspis*. The collection site is subtropical rainforest at c. 950 m altitude, and all available material was taken by fogging the rainforest trees *Dysoxylum rufum* (Rich.) Benth. and *Synoum glandulosum* (Smith) Juss. (both Meliacene).

Platycolaspis mcquillani sp. nov.

Figures 2, 7, 8, 12, 16–18, 25–27, 31, 36, 43

Types. Holotype: ♂ / 41°50'S 146°03'E Pelion Hut, 3 km S Mt Oakleigh TAS, 860 m 30.Nov.1990–8.Jan.1991 E. Nielsen, E. Edwards malaise no. 5, closed forest/ (ANIC).

Paratypes (89 specimens, all Tasmania): 15, same data as holotype (ANIC); 21, same data as holotype, except 8.Jan–12 Feb.1992, A. Calder and W. Dressler (ANIC, SAM); 1, as above except, FIT no 1 (ANIC); 1, as above except, malaise no 2 (ANIC); 4, as above except, 30.Nov.1990–8.Jan.1991, E. Nielsen and E. Edwards, malaise no 4; 2, as above except, malaise no 2; 1, as above except 28–30.Nov.1990, T. Weir, beating *Nothofagus* (ANIC); 1, as above except, on grass and low vegetation (ANIC); 1, as above except, 12–15.Feb.1991, A. Calder and W. Dressler, sweeping grass tufts (ANIC); 4 / 41°52'S 146°03'E 2 km NNE Mt Ossa, 1000 m, 30.Nov–8.Jan.1991, E. Nielsen and E. Edwards, FIT no 3/ (ANIC); 10, / 41°51'S 146°03'E 4 km S Mt Oakleigh, 880 m, 30.Nov—8.Jan.1991, E. Nielsen and E. Edwards, malaise no 3/ (ANIC); 2, / Hartz Mtns NP 800 m on *Noth. cunninghamii* 7.Dec.1986 P. B. McQuillan / (ANIC); 2♂, 6♀ 42°.39'S 146°.34'E 0.5 km NW Lake Webster, Mt Field NP on *Noth. cunninghamii* 920 m 7.Feb.1992 C. Reid/ (ANIC); 10♂, 8♀ / 42°40'S 146°41'E 2.5 km W National Park, Mt Field NP, on *Noth. cunninghamii*, rainf., 600 m, 6.Feb.1992 C. Reid/ (ANIC).

Other material examined. 4♂, 5♀ / 42°39'S 146°33'E W side Walker Tarn, Mt Field NP TAS on *Noth. gunni* 1140 m 7.Feb.1992 C. Reid/ (ANIC).

Diagnosis. Entire upper surface glabrous or minute setae visible at apex of elytra; sides of pronotum not angulate; procoxal cavities closed or apparently so; prosternal process broad, medial width at least half procoxal cavity length.

Description. Colour: male entirely yellowish- to reddish-brown except abdomen, tarsi and palpi dark brown to black and antennal segments 6–11 and apex of 5 black; venter of thorax, base of femora and sides of head may also be dark brown to black; female entirely yellowish- or reddish-brown, except palpi and antennae as male. The 9 specimens from Walker Tarn are generally darker brown, and more extensively black ventrally. Pubescence: dorsum glabrous, but with minute stubs of setae in punctures, venter with short but conspicuous pubescence. Size: male 1.7–2.4 mm, female 2.3–2.8 mm. The Walker Tarn specimens are generally larger: male 2.25–2.4 mm, female 2.8–3.0 mm.

Head and pronotum densely punctured and microsculptured, punctures deep, with narrow convex interspaces; interocular space about 2–2.5 times eye length; frontoclypeus shining but shallowly microsculptured; antenna (Fig. 7) slightly more than half body length, segments 6–11 expanded towards apex, slightly more elongate in the Walker tarn specimens; last segment of maxillary palp slightly contracted to truncate apex; explanate lateral margins of pronotum (Fig. 2) distinct, evenly curved to broad front-angles; pronotum with transverse median depression continuous or rarely divided by narrow median convexity; fore coxal cavities (Fig. 12) closed by overlap or touching of prosternal process on hypomeral lobe; prosternal process slightly elongate, medial width 0.5–0.75 coxal cavity length; apex of process curved.

Elytra (Fig. 2): strongly and closely punctured, subseriate, with about 5 irregular shallow longitudinal ridges, including raised, evenly convex, interstice from shoulder; epipleura at c. 45° to vertical; apex of elytra abruptly sloped in profile; scutellum equilateral–triangular with rounded apex;

Male: aedeagal median lobe (Figs 25–27) relatively thick with evenly curved dorsal surface and produced apex in profile; apex broadly but strongly mucronate, with about 15–20 scattered short dorsal setae, 0.2 or less width of median lobe (size and distribution of setae variable).

Female: vaginal palp (Fig. 31) ovate with angular basal margin and broadly rounded tip; spermatheca (Fig. 36) broad U-shaped, with elongate, strongly reflexed collum; kotpresse (Fig. 43) elongate–triangular dorsal transverse sclerites narrowly laterally prominent, ventral sclerite slightly lengthened medially and expanded but only weakly prominent at sides.

Distribution and biology. This species is only known from three areas in Tasmania where it feeds on new foliage of *Nothofagus cunninghamii*. The Walker Tarn specimens were feeding on young foliage of *N. gunni*. All specimens were taken at moderate to high altitude (600–1140 m).

Remarks. The specimens from Walker Tarn differ in size and, to a lesser extent, colour from all other material, as described above. These specimens were also taken on a different foodplant (*N. gunni*) and at a higher elevation (1140 m; other specimens 600–920 m). I have not been able to detect any obvious constant differences in external or genital morphology between the Walker Tarn specimens and the other material available, and therefore prefer to regard all this material as belonging to *P. mcquillani*, but exclude the Walker Tarn specimens from the type series.

Platycolaspis pubescens sp. nov.

Figures 3, 13, 15, 22, 23, 32, 37–39, 44, 45

Types. Holotype ♂: /42°06'S 146°10'E Lake St. Clair 750 m TAS 25–27 Jan 1980, Lawrence and Weir / Pyrethrum spray tree ferns / [ANIC].

Paratypes (54): Tasmania: 1♂ /42°10'S 146°07'E 4 km SSE of Mt Rufus 800 m, 26–28 Jan 1980, Lawrence and Weir/ by beating / [ANIC]; 1♀ / 2.5 km W National Park, Mt. Field, 42°40'S 146°41'E, *Noth. cunninghamii*, rainf. 600 m 6.Feb.1992, C. Reid (ANIC); 1♂ / Hartz Mts NP Hartz Rd 740 m 8–10 Feb. 1980 *Euc. — Nothofagus* A. Newton M. Thayer / pyrethrin fogging *Nothofagus cunninghami* bark / [ANIC]; 2 / 41°50'S 146°03'E Pelion Hut, 3 km S Mt Oakleigh 860 m 30.Nov.1990–8.Jan.1991 E. Nielsen, E. Edwards malaise no. 5, closed forest / (ANIC); 1, as above except, 8.Jan–12.Feb.1991, A. Calder and W. Dressler, malaise no 1 (ANIC); 2, as above except, malaise no 5 (ANIC); 1 / 41°51'S 146°03'E 4 km S Mt Oakleigh, 880 m, 30.Nov—8.Jan.1991, E. Nielsen and E. Edwards, malaise no 3, closed forest/ (ANIC); 2 /Hartz Mtns NP 800 m on *Noth. cunninghamii* 7.Dec.1986 P. B. McQuillan / (ANIC); 1♂ / 42°10'S 146°08'E 9 km WSW Derwent Bridge 21 Jan 1983 I. Naumann, J. Cardale / [ANIC]; 1♂ /Tasmania Simson/ [SAM]; 6 / Tasmania Simson / 3802 / [SAM]; 2 / Tasmania Blackburn / 3802 / [SAM]; 10 / Mt Wellington Tas: Lea / [SAM]; 2 /Mt Wellington Tas: Lea / moss / el. distinctly pubesc. distings. from 10336 / [SAM]; 1 / Waratah Tas: Lea / [SAM]; 6 / King I. Tas: Lea / 10941 / probably n. g. of eumolpids [t?] Jacoby / note abd. fovea of specimen in front of pin / [SAM]; 2 / Launceston 3.Nov.94 / [SAM]; 2 / King I., ? partly abraded 10941 / [SAM]; 3 / Launceston Tas: Lea/ (TAIC).

Victoria: 1♂ / 37°34'S 145°53'E Cumberland Ck 13 km ESE Marysville 18 Jan 1978 V. Lawrence and Weir / by beating / [ANIC]; 1♂ 1♀ / Barwon Heads 4.Nov.44 E. Smith / [NMV]; 2 / Nelson, V. Blackburn / [SAM].

South Australia: 1 / Mt Gambier S. Australia Lea / [SAM]; 1 / Mt Gambier S. Australia Lea / *Platycolaspis australis* Jac. / [SAM].

Diagnosis. Head and pronotum covered in close recumbent pubescence, erect or recurved and in rows on elytra; head and pronotum densely, rugosely punctured, interspaces ridged; pronotum with single transverse depression across middle; explanate margins of pronotum narrow, slightly angled; procoxal cavities closed in ventral view; apex of elytra abruptly declined in side view.

Description. Colour: ground colour yellowish-brown, most specimens with elytra vaguely darkened around scutellum and obliquely across apical half; palpi yellowish-brown to brown; male antennal segments 6–11, tarsi, middle of femora, abdomen and metathorax blackish-brown, head reddish-brown; female paler, with yellowish-brown tarsi, but may have blackish-brown metathorax. Pubescence: head and pronotum densely pubescent with long recumbent setae, elytra with setae arranged in 5–6 rows on each elytron with scattered setae on intervals, elytral setae either erect or recumbent; venter pubescent. Size: male 1.6–2.0 mm; female 2.0–2.5 mm.

Head and pronotum (Fig. 3) densely but finely punctured and strongly microsculptured, punctures separated by narrow ridges; eyes large and convex, interocular space about twice eye length; frontoclypeus dull, strongly microsculptured (1 specimen from King Island with shining frontoclypeus); antenna half body length, segments 7–11 expanded towards apex; last segment of male maxillary palp broadly expanded to apex, in female parallel-sided with truncate apex; explanate lateral margins of pronotum distinct, evenly curved to slightly angulate at midpoint and broad at front angles; pronotum with continuous transverse median depression (Fig. 15); fore coxal cavities (Fig. 13) closed by overlap or touching of prosternal process on hypomeral lobe; prosternal process quadrate to slightly elongate, medial width almost coxal cavity length; process angulate to triangularly pointed at apex.

Elytra (Figs 3, 15): strongly and closely punctured, subseriate, diameter of punctures more than twice pronotal punctures; with about 5 irregular shallow longitudinal ridges, including raised interstice from shoulder, or these ridges absent; epipleura at 45° to vertical; apex of elytra abruptly sloped in profile; scutellum equilateral–triangular, with rounded apex.

Male: aedeagal median lobe (Figs 22–23) in profile with a prominent convexity on dorsal surface, a third from apex; ventral surface almost straight; apex almost right-angled with blunt tip, and with 10–12 scattered setae, 4 longer, c. 0.2 width of median lobe.

Female: vaginal palp (Fig. 32) ovate to elongate–ovate, with broadly rounded tip; spermatheca (Figs 37–39) variable, but slightly V-shaped, usually with recurved tip and collum oblique

from base; kotpresse (Figs 44–45) dorsal transverse sclerites variably triangular, only slightly laterally prominent, ventral sclerite almost parallel-sided, laterally prominences variably crenulate.

Distribution and biology. This species is recorded in south-eastern Australia from Mount Gambier to Marysville, Tasmania (where it is predominantly western) and King I., and has been collected in November, January (most records) and February.

No hosts are recorded. It may feed on *Acacia* flowers, like *P. australis*, but it is frequently collected in association with *Nothofagus cunninghamii* and is a much duller brown species than *P. australis*. However the range of *P. pubescens* extends well beyond the range of *N. cunninghamii*, which is absent from west Victoria.

Remarks. This is variable and it has been difficult to determine whether one or two species are represented in the material to hand. I have dissected specimens from Barwon Heads, Derwent Bridge, King I., Launceston, Mt Rufus and Mt Wellington. These specimens vary slightly in colour, elytral pubescence, shape of lateral pronotal margins, development of elytral ridges and shape of spermatheca. Males from all localities have the prominent swelling on the dorsal surface of the median lobe, which is considered to be diagnostic for the species.

Acknowledgements

I thank the following curators for the loan of material in their care: John Lawrence (ANIC), Eric Matthews (SAM), Peter McQuillan (TAIC), Margaret Schneider (UQIC), Sharon Shute (BMNH), and Ken Walker (NMV). Roger Kitching (Griffith University) allowed me to use the series of specimens from Lamington NP. Kathy Pickerd, Helen Geier (CSIRO) and Keith Herbert (ANU) helped with the SEM photography, and Peter Cranston (CSIRO), Penny Gullan (ANU) and John Lawrence gave helpful criticism of the manuscript. This work was supported by a grant from the Australian Biological Resources Study and the use of facilities at the Australian National Insect Collection, CSIRO, Canberra.

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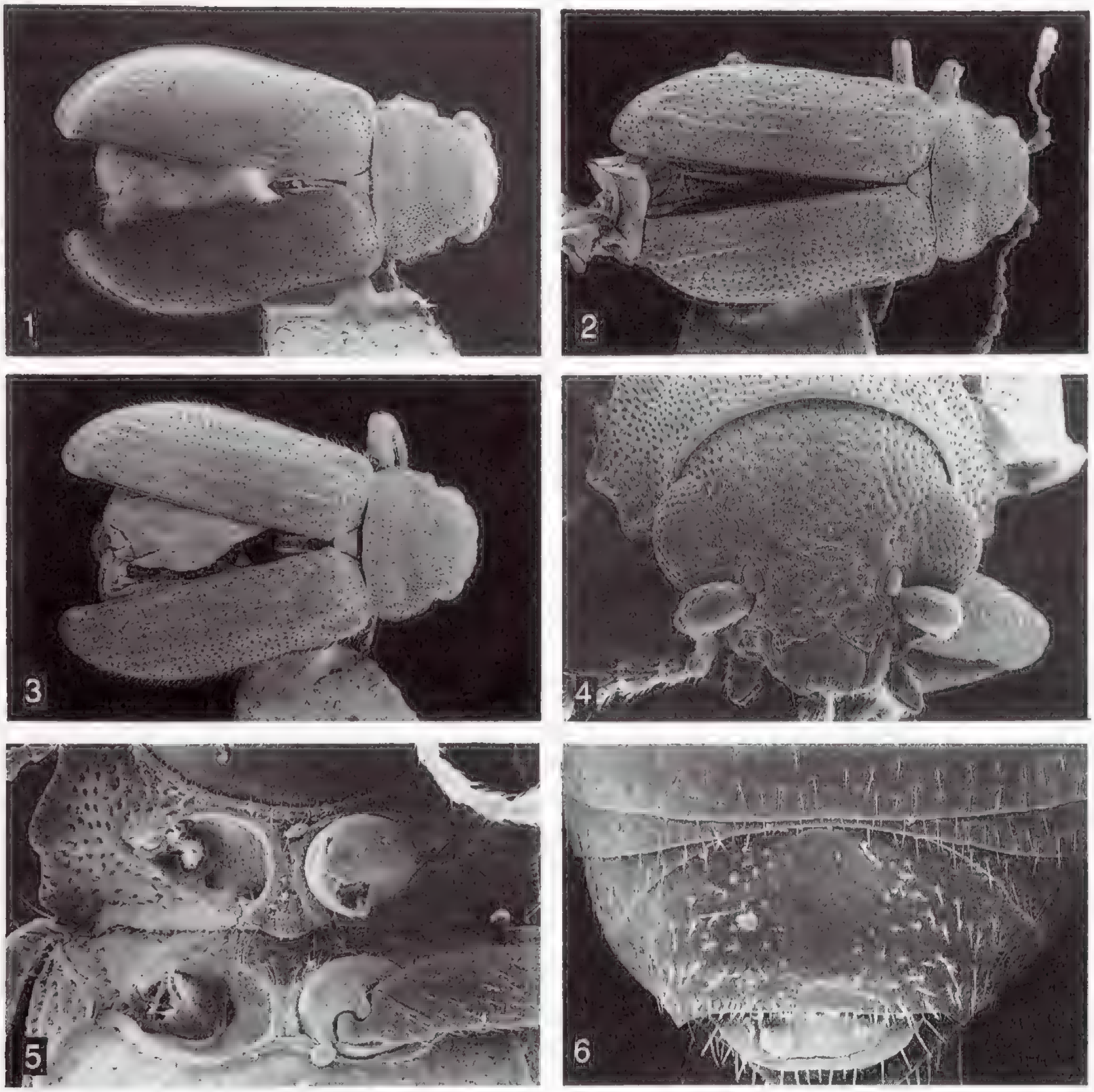
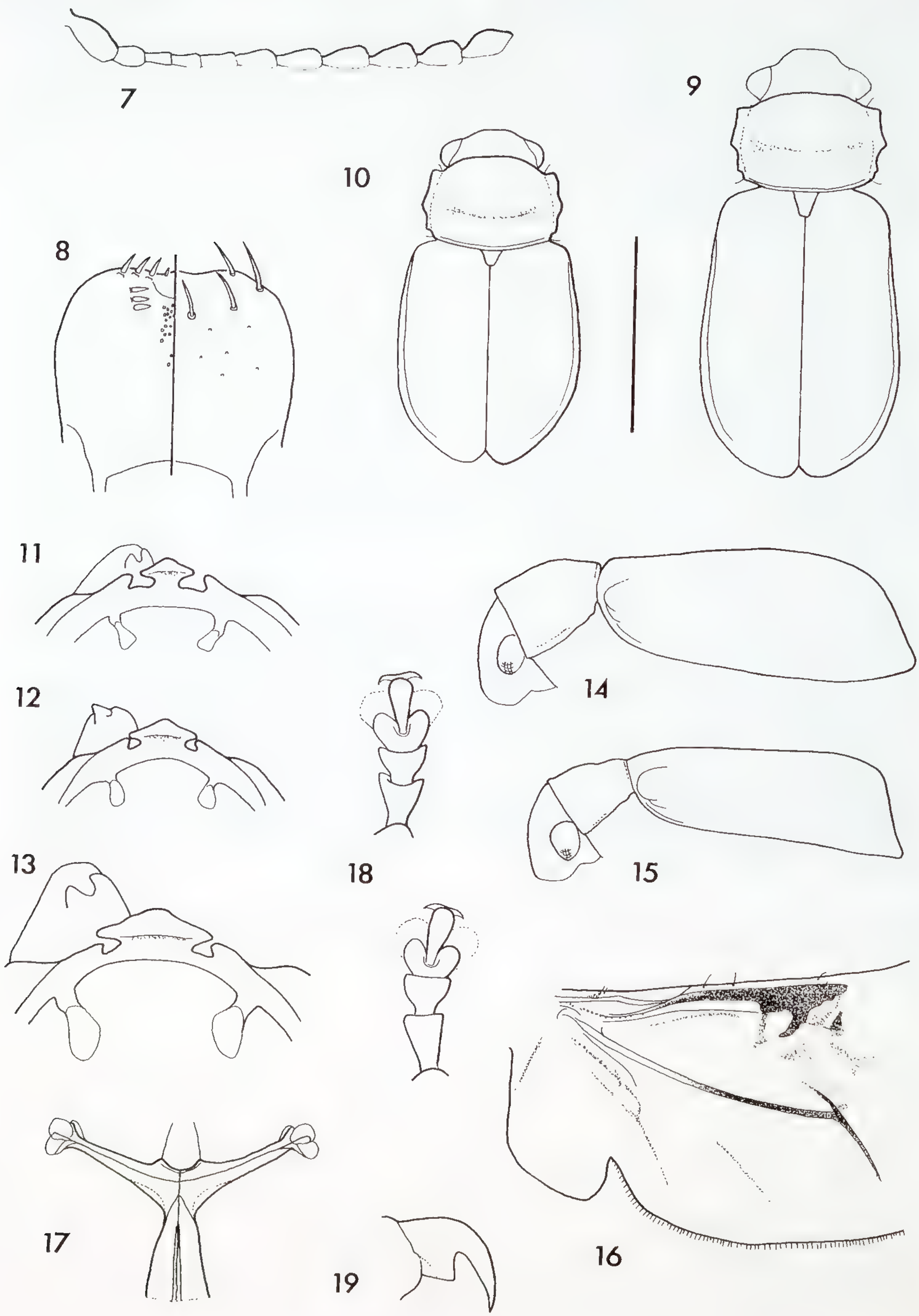


Figures 1–6. *Platycolaspis* spp.male habitus of *P. australis* (1), *P. mcquillani* (2) and *P. pubescens* (3); *P. australis*, male head (4), female venter of thorax (5), female apex of abdominal venter (6).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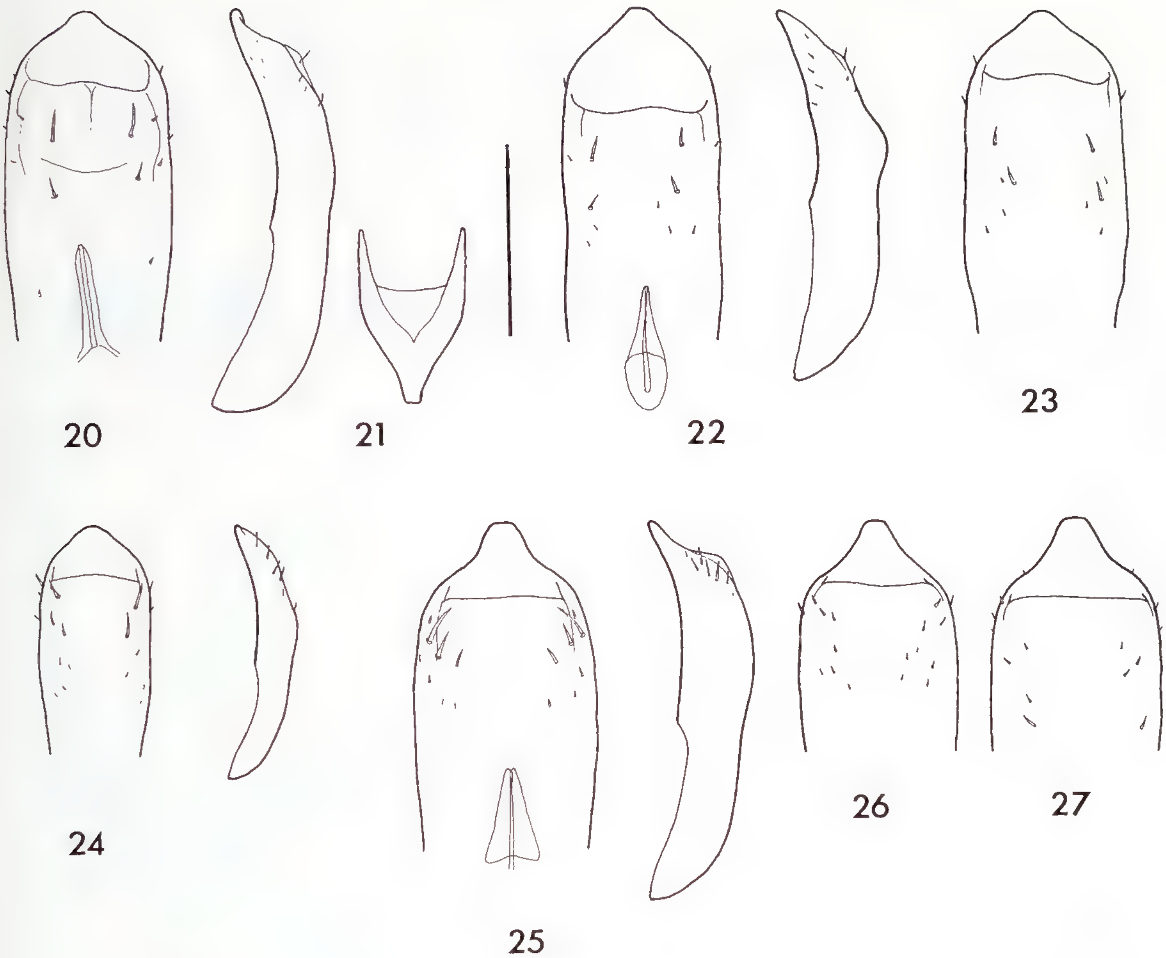
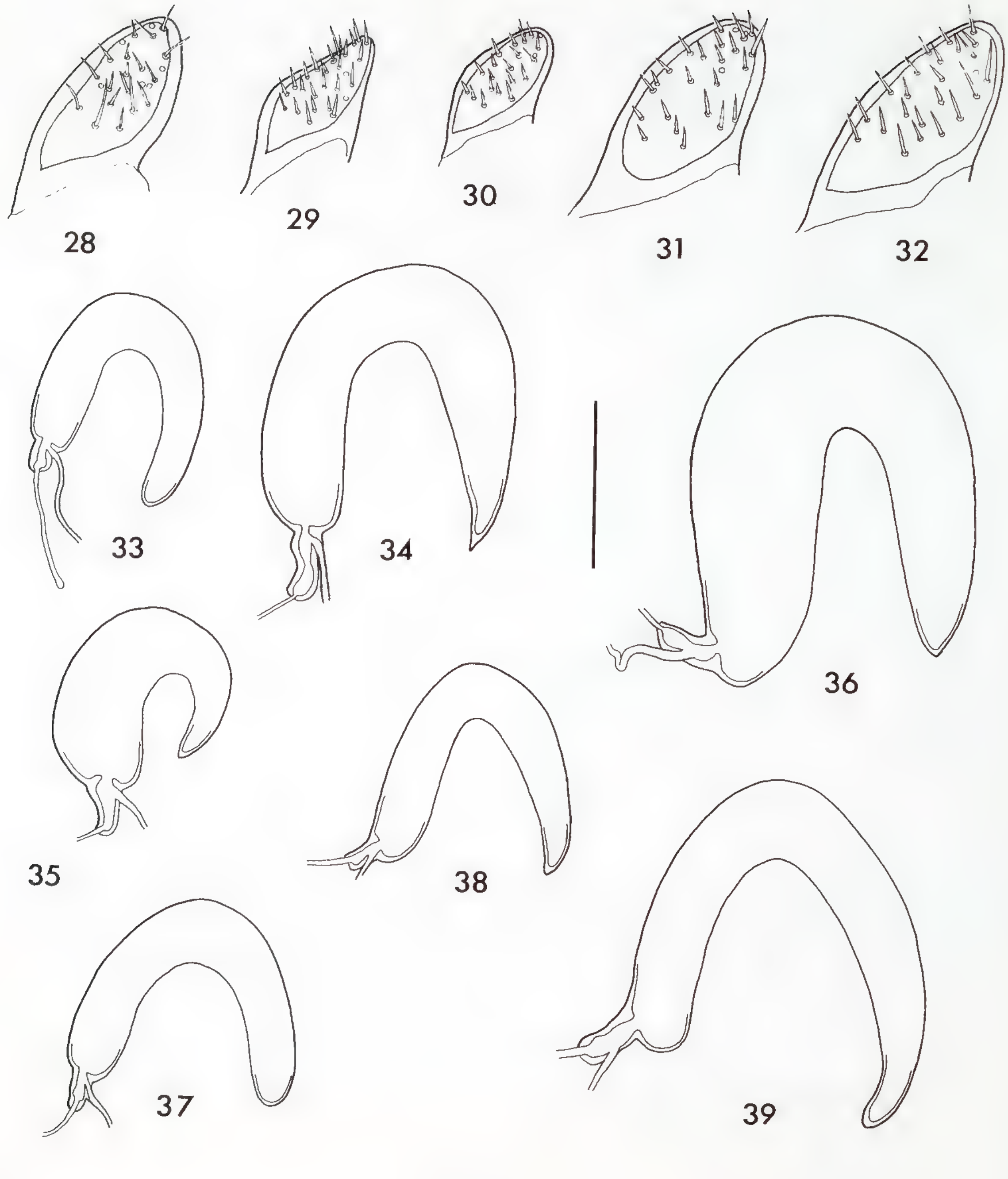


Figures 20–27. Aedeagus of *Platycolaspis* spp. Median lobe, dorsal and lateral, or dorsal only, of *P. australis* (20), *P. pubescens*, Launceston (22), *P. pubescens*, Barwon Heads (23), *P. lamingtonensis* (24), *P. mcquillani*, Pelion Hut (25), *P. mcquillani*, Mount Field, *Nothofagus cunninghamii* (26), *P. mcquillani*, *Nothofagus gunni* (27); tegmen of *P. australis* (21). Scale = 0.1 mm (dorsal view), 0.25 mm (lateral and tegmen).

←

Figures 7–19. *Platycolaspis* spp. Antenna (7) and labrum, epipharynx left, dorsum right (8) of *P. mcquillani*, Pelion Hut; male dorsum of *P. australis* (9) and *P. lamingtonensis* (10); posterior view of prothoracic venter of *P. australis* (11), *P. mcquillani* (12) and *P. pubescens* (13); dorsal profile of *P. alpina* (14) and *P. pubescens* (15); basal half of wing of *P. mcquillani* (16); metendosternite of *P. mcquillani* (17); male fore (top) and hind tarsus of *P. mcquillani* (18); claw of *P. australis* (19). Scale = 1.0 mm (9, 10, 14, 15), 0.8 mm (16), 0.4 mm (7, 11–13, 17, 18), 0.125 mm (8), or 0.1 mm (19).



Figures 28–39. *Platycolaspis* spp. Left vaginal palp of *P. alpina* (28), *P. australis* (29), *P. lamingtonensis* (30), *P. mcquillani* (31) and *P. pubescens* (32); spermatheca of *P. alpina* (33), *P. australis* (34), *P. lamingtonensis* (35), *P. mcquillani* (36), *P. pubescens*, Barwon Heads (37), *P. pubescens*, King I. (38), and *P. pubescens*, Mt Wellington (39). Scale = 0.1 mm.

Figures 40–45. *Platycolaspis* spp. Dorsal (left) and ventral of ♀ rectum of *P. alpina* (40), *P. australis* (41), *P. lamingtonensis* (42), *P. mcquillani* (43), *P. pubescens*, Barwon Heads (44), and *P. pubescens*, Mt Wellington (45). Scale = 0.2 mm.

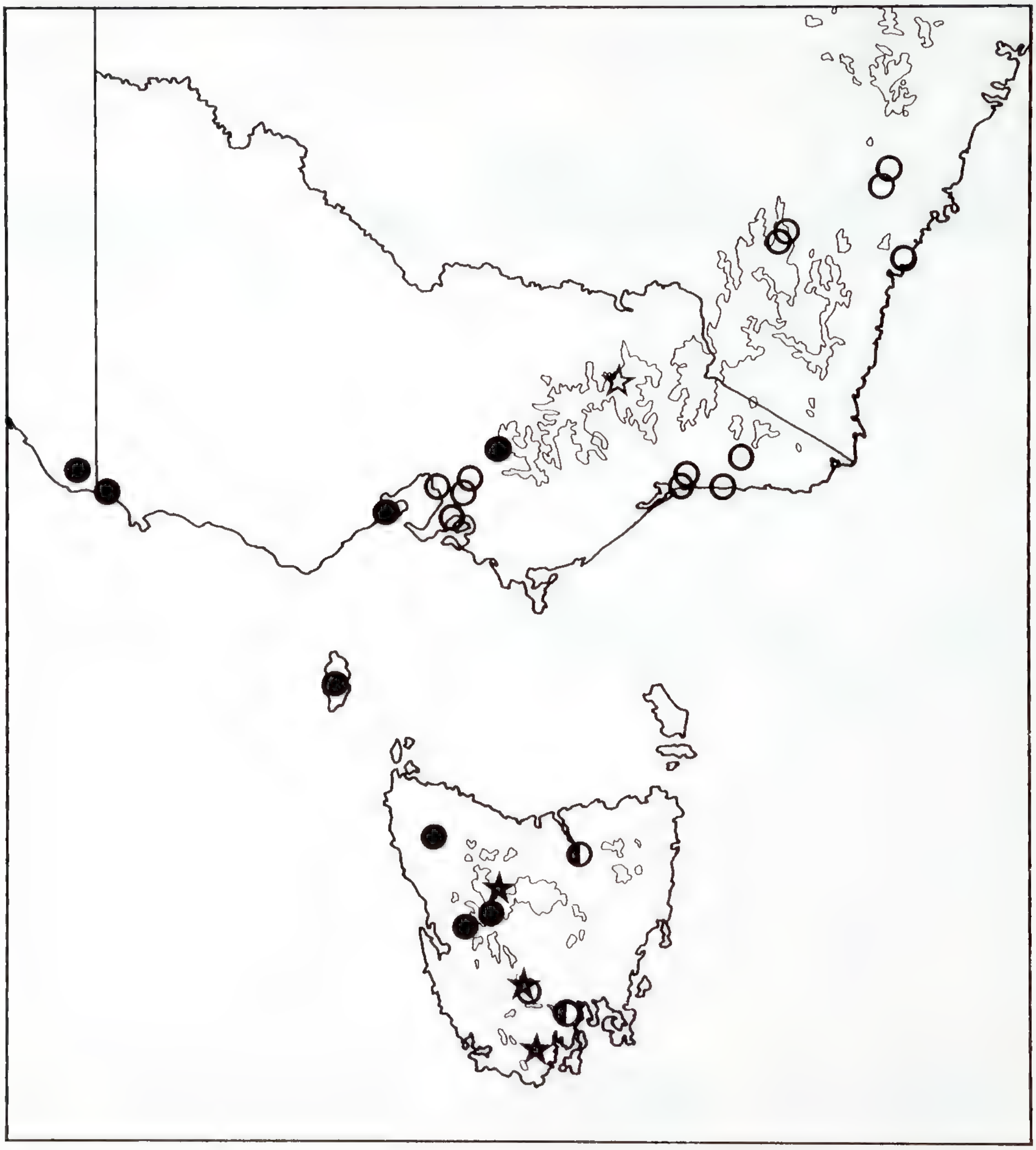


Figure 46. South-eastern Australia, showing distribution of *Platycolaspis* spp. (except *P. lamingtonensis*) ☆= *P. alpina*; ○= *P. australis*, ◐= *P. australis* and *P. pubescens*, ★= *P. mcquillani* and *P. pubescens*, ●= *P. pubescens*. Fine line = 500 m contour.

Memoirs of the Museum of Victoria 54: 221–242 (1994)

SYNOPSIS OF *PARELEDONE* AND *MEGALELEDONE* SPECIES, WITH DESCRIPTION OF TWO NEW SPECIES FROM EAST ANTARCTICA (CEPHALOPODA: OCTOPODIDAE)

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Abstract

Lu, C.C. and Stranks, T.N., 1994. Synopsis of *Pareledone* and *Megaleledone* species, with description of two new species from East Antarctica (Cephalopoda: Octopodidae). *Memoirs of the Museum of Victoria* 54: 221–242.

A synopsis is given for species of the genus *Pareledone* from Prydz Bay, Antarctica: *P. adelieana* (Berry, 1917), *P. charcoti* (Joubin, 1905), and *P. harrissoni* (Berry, 1917). Two new species of *Pareledone* are described and illustrated: *P. framensis* from Fram Bank, off MacRobertson Land, and *P. prydzensis* from Prydz Bay, off the Amery Ice Shelf, Antarctica. A comparative description of *Megaleledone senoi* Taki, 1961, from Antarctica is also provided.

Introduction

The taxonomy of Antarctic eledonine octopuses is poorly known. A literature review revealed that eight nominal species of *Pareledone* have been previously described from Antarctic waters (latitudes greater than 60°S). Several of the species (e.g., *Pareledone antarctica* (Thiele, 1920), *P. aurorae* (Berry, 1917), and *P. umitakae* Taki, 1961) were known only from type material, and most other species have not been reviewed in detail since Robson's (1932) monograph. Much of the past work on Antarctic octopods has concentrated on material from the Antarctic Peninsula vicinity, and little information has been published on the fauna of East Antarctica.

A study is now being undertaken to provide systematic information on octopods of the Prydz Bay region (around 68°S, 75°E). While attempting to identify the *Pareledone* specimens, it became clear that two previously undescribed species existed among the specimens collected. This paper describes the new species and provides a comparison with existing valid species of *Pareledone* from the region.

Voss (in Palacio, 1978) considered that *Megaleledone* (a monotypic genus) was a synonym of *Pareledone*, so the new species here diagnosed are also contrasted with *Megaleledone senoi* Taki, 1961. Further systematic information on the *Pareledone* and *Megaleledone* species will be provided with the future publication of a larger revision of the Octopodidae of the Prydz Bay region.

Material and methods

A collection of 125 eledonine octopuses from 41 stations on the continental shelf (water depths less than 1000m) has been accumulated during benthic surveys conducted by the Australian National Antarctic Research Expeditions (ANARE). Fauna has been sampled by beam or otter trawls and epibenthic sleds, during cruises of the MS *Nella Dan* (1985-1987) and RSV *Aurora Australis* (1990 onwards). Live octopuses were observed during the 1991 cruise of RSV *Aurora Australis* to Prydz Bay; these animals were then sacrificed using fresh water, fixed in formalin, and preserved in ethanol. A number of animals were autopsied for parasites and the material has been forwarded to appropriate researchers for identification and description.

Holotypes and most paratypes have been deposited at the Museum of Victoria; paratypes and other voucher specimens were deposited at the Australian Museum, and the National Museum of Natural History, Smithsonian Institution.

Efforts were made to verify most of the previous type and nontype records. Where specimens have not yet been available for study, or descriptions are not clear, the relevant entry in the synonymy has been denoted with a question mark (?).

Where there is sufficient material, counts and measurements are included for a representative 10 females and 10 males. Counts, measurements and indices were defined by Roper and Voss (1983) and Toll (1988) with the following exception: OASC — opposite arm sucker count in

males, or sucker count on either arm L3 or R3 in females. Materials studied, including type specimens, are from: The Australian Museum, Sydney (AM); Muséum National d'Histoire Naturelle, Paris (MNHN); Museum of Victoria, Melbourne (NMV); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Octopodidae

Pareledone Robson, 1932

Type species. Eledone charcoti Joubin, 1905.

Diagnosis. Benthic octopodids. Mantle saccular, without fins. Eight arms lacking cirri, arms with small uniserial suckers, third right arm of males hectocotylised with end of arm clearly differentiated into ligula and calamus, arms tips not otherwise modified. Web well developed. Funnel organ VV- or W-shaped. Gills well developed, with 6–9 lamellae. Ink sac present. Crop well developed. Radula normal, with multicuspid rhachidian, lateral teeth and marginal plates well defined. Cartilaginous stylets absent.

Pareledone adelieana (Berry)

Figures 1, 9a–d

Moschites adelieana Berry, 1917: 17, text figs 10–13, pl. 11 fig. 5, pl. 12 figs 6–8.

Pareledone adelieana. — Robson, 1932: 278.

Pareledone adeliana [*sic*]. — ?Dell, 1959: 92, text fig. 7. — Voss, 1988: 300 [designation of *nomen dubium*].

Pareledone umitakae Taki, 1961: 308, text figs 9–16, pl. 3.

Material examined. Holotype: Antarctica, off Mertz Glacier (66°55'S, 145°21'E), 288–300 fm [527–549 m], SY *Aurora*, Stn 2, Australasian Antarctic Expedition, 28 Dec 1913, AM C40889 (submature ♀, 29.5 mm ML).

Other material examined: Antarctica, off Enderby Land: 65°50'S, 50°34'E, 540 m, MS *Nella Dan*, Stn HRD-011, ANARE, M. D. Norman, 20 Nov 1985, NMV F65629 (submature ♀, 17.7 mm ML); 65°56'S, 50°52'E, 386–400 m, MS *Nella Dan*, Stn HRD-010, ANARE, M. D. Norman, 15 Nov 1985, NMV F65628 (mature ♂, 54.5 mm ML).

Off MacRobertson Coast: 67°15'S, 68°56'E, 139 m, RSV *Aurora Australis*, Stn AA91-99, ANARE, C. C. Lu and T. N. Stranks, 28 Feb 1991, NMV F65611 (immature ♂, 36.0 mm ML); 67°15'S, 70°07'E, 172–182 m, RSV *Aurora Australis*, Stn AA91-95, ANARE, C. C. Lu and T. N. Stranks, 26 Feb 1991, NMV F65670 (immature ♂, 24.8 mm ML); 67°07'S, 70°17'E, 256 m, ANARE, 2 Feb 1986, NMV F65627 (mature ♂, 59.0 mm ML); 67°03'S, 70°24'E, 242–244 m, RSV *Aurora Australis*, Stn AA91-96, ANARE, C. C. Lu and T. N. Stranks, 26 Feb 1991, NMV F65669 (immature ♂, 28.4 mm ML); 66°53'S, 70°44'E, 444–453 m, RSV *Aurora Australis*, Stn AA91-97, ANARE, C. C. Lu and T. N. Stranks, 26 Feb 1991, NMV F65668 (submature ♀, 26.7 mm ML).

Off Amery Ice Shelf, Prydz Bay: 67°42'S, 71°56'E, 667–676 m, RSV *Aurora Australis*, Stn AA91-92, ANARE, C. C. Lu and T. N. Stranks, 25 Feb 1991, NMV F65613 (immature ♂, 29.0 and 31.4 mm ML); 66°48'S, 72°33'E, 526–532 m, RSV *Aurora Australis*, Stn AA91-89(2), ANARE, C. C. Lu and T. N. Stranks, 24 Feb 1991, NMV F65630 (submature ♀, 21.7, 23.5, 27.1, 30.5, 35.1, 35.7, 39.6 mm ML; mature ♀, 46.8 mm ML; spent ♀, 43.1 mm ML; immature ♂, 25.4, 27.6, 29.7, 47.4 mm ML; mature ♂, 38.3, 40.8 mm ML), USNM 884248 (mature ♂, 44.8 mm ML); 66°59'S, 72°37'E, 532–536 m, RSV *Aurora Australis*, Stn AA91-90, ANARE, C. C. Lu and T. N. Stranks, 24 Feb 1991, NMV F65671 (submature ♀, 23.3 mm ML); 67°56'S, 76°24'E, 436–441 m, RSV *Aurora Australis*, Stn AA91-77, ANARE, C. C. Lu and T. N. Stranks, 18 Feb 1991, NMV F65612 (immature ♂, 40.5 mm ML).

Diagnosis. Medium sized animals (ML to 55 mm; TL to 160 mm) (fig. 1); mantle elongate ovoid (MWI 62.7–*76.1*–91.1); head wide, usually slightly wider than mantle (HWI 67.8–*77.3*–91.6), demarked from mantle by moderate constriction; eyes very large, project above surface of head. Funnel large, stout, bluntly tapered (FuLI 29.1–*34.4*–41.3); funnel organ W-shaped, limbs thick, outer limbs as long as median limbs (fig. 9c). Mantle aperture very wide (PAI 93.6–*104.3*–128.2). Arms short (MAI 45.3–*58.4*–81.5) (1.9–2.2 times ML in mature animals), stout, tapering to narrow tips. Arm lengths subequal, arm order usually 4.3.2.1 (ALI, arm 1: 112.9–*154.6*–205.2; arm 2: 115.0–*161.8*–216.5; arm 3: 117.6–*165.0*–214.2; arm 4: 112.4–*168.1*–221.0). Arm suckers uniserial, raised from arm surface, small (ASI 4.3–*6.8*–10.1), without sucker enlargement. Third right arm of males hectocotylised, shorter than its opposite number (OAI 81.2–*91.5*–98.0; HcAI 131.0–*156.1*–171.0); ligula medium size, 9–15% of third right arm length in mature animals (LLI 9.7–*12.8*–15.0); ligula groove long, well marked and deep, with approximately 8 transverse ridges; calamus long, pointed (CaLI 45.1–*45.4*–46.6) (figs 9a, b); hectocotylised arm with 22–28 suckers; opposite arm with 26–46 suckers. Web moderately deep (WDI 21.2–*27.1*–32.5), web formula usually B=C=DAE. Ink sac present. Gill lamellae 6–7. Mature ovarian eggs, from female with enlarged ovary, large (8–9 mm long, 3–4 mm wide) (EgLI 17.3–*17.9*–18.4; EgWI 7.1–*7.3*–7.5). Male with long penis (PLI 25.7–*29.9*–39.5), with single coiled diverticulum (fig. 9d); spermatophores moderately long (SpLI 58.7–*66.9*–78.7), slender (SpWI 4.9–*5.5*–6.2), with large, coiled sperm reservoir (SpRI 33.3–*40.0*–45.0).

Integumental sculpture consists of pattern of fine, rounded and widely scattered papillae on

Figure 1. *Pareledone adelieana* (Berry): a, dorsal, and b, lateral, view of USNM 884248, ♂, 44.8 mm ML.

dorsal surface; papillae absent from ventral surface. Large unbranched primary papillae present in ocular region, with one large supraocular papilla. Two short, longitudinal integumentary ridges present on mid-dorsal posterior mantle. Ventrolateral integumentary ridge around mantle circumference present. In life, colour of resting animals uniformly purple–pink to purple–grey dorsally, white to cream–white ventrally. When stimulated, animals become darker in colour, uniformly purple–red to purple–brown dorsally, cream–white ventrally. White spots consist of one spot on mid-dorsal brachial crown, and one broad spot on mid-dorsal mantle. White transverse bar present between eyes. Ocelli absent.

Males mature at approximately 40mm ML. Females attain ovarian maturity at about 45mm ML.

Distribution. East Antarctica, from off Dronning Maud Land (67°52'S, 33°14'E) (Taki, 1961); from off Enderby Land (65°50'S to 65°56'S, 50°34'E to 50°52'E), off MacRobertson Land (66°53'S to 67°15'S, 68°56'E to 70°44'E), off the Amery Ice Shelf, Prydz Bay (66°48'S to 67°56'S, 71°56'E to 76°24'E) (this study); and from off the Mertz Glacier (66°55'S, 145°21'E) (Berry, 1917). Other published records need to be verified, but the species is probably restricted in distribution to East Antarctic waters. The species has been collected from the Antarctic continental shelf at depths ranging from 139–680m, with temperatures from -2.2 to -1.7°C, on mud and sand bottoms with pebbles and rocks, and among sponges, bryozoans and gorgonaceans.

Remarks. Voss' (1988) designation of *Pareledone adelieana* as a *nomen dubium* appeared without justification for the decision, and it is unclear whether he studied material first-hand. The holotype of *P. adelieana* (Berry) was examined for the present study. The mantle was found to be distorted through preservation and contracted longitudinally, resulting in the mantle length being much shorter (and the mantle width much wider) than would have existed in the live animal. The typical morphology, with the very large eyes, wide head and narrow elongate mantle, is shown in Fig. 1. Additional morphological measurements and counts of the type have permitted the species to be clearly characterised. The two syntypes of *P. umitakae* Taki have not been available for study. The material may still be extant in the Taki family collection at Kyoto, Japan (T. Kubodera, National Science Museum, Tokyo, pers. comm.). However, Taki's (1961) detailed description leaves us in no doubt that *P. umitakae* is a junior synonym of *P. adelieana*.

P. adelieana does not appear to be closely related to the other species of *Pareledone* described here. The elongate mantle, wide head, very large eyes, W-shaped funnel organ, short and stout arms, and ribbed ligula groove of *P. adelieana* are at the extremes of the morphological ranges of *Pareledone* species in general. In the future, removal of this species from the *Pareledone* genus may be justified.

Pareledone charcoti (Joubin)

Figures 2, 9e–h

Eledone charcoti Joubin, 1905: 22, pl. 3 figs 1, 2. — Joubin, 1906: 2, pl. 1 figs 1, 2. — ?Joubin, 1914: 35, text figs 1, 2. — ?Odhner, 1923: 6.

[?]*Moschites charcoti*. — Hoyle, 1912: 97, text figs 6, 7. — Massy, 1916: 151, text figs 12–21.

Moschites aurorae Berry, 1917: 20, text figs 14–20, pl. 12 fig. 9, pl. 13 figs 10–12 [also refer to postscript, 1918].

[?]*Graneledone charcoti*. — Robson, 1930: 388.

[?]*Pareledone charcoti*. — Robson, 1932: 270. — Dell, 1959: 93, text figs 4–6. — Roper et al., 1985: 200. — Okutani, 1986: 279, pl. 3 figs 25, 26. — Dong, 1991: 183, text fig. 1.

Material examined. Lectotype (designated by Robson, 1932): Antarctica, off Graham Land, Booth Island [65°05'S, 63°55'W] [as 'Ile Wandel, Antarctique'], on the beach among algae and pebbles, 'Français,' Expedition Antarctique Française, 3 Sep 1904, MNHN 5–7–1095 (submature ♀, 33.8mm ML).

Other material examined: Antarctica, off Queen Mary Land (66°08'S, 94°17'E), 120fm, [220m], SY *Aurora*, Stn 8, Australasian Antarctic Expedition, 27 Jan 1914, AM C40891 (immature ♂, 27.7mm ML) (holotype of *Moschites aurorae* Berry, 1917).

Off Enderby Land: 65°56'S, 50°52'E, 386–400m, MS *Nella Dan*, Stn HRD-10, ANARE, M. D. Norman, 15 Nov 1985, NMV F65688 (submature ♀, 16.4 and 31.3mm ML; immature ♂, 16.7 and 18.4mm ML).

Off MacRobertson Land: 66°59'S, 62°49'E, 117m, ANARE, 6 Feb 1986, NMV F65689 (submature ♀, 38.7 and 39.6mm ML; immature ♂, 30.6mm ML; mature ♂, 46.8 and 65.1mm ML); Horseshoe Harbour, Mawson Station [67°40'S, 63°00'E], ANARE, J. S. Bunt, 16 Jan 1957, NMV F23493 (♂, 40.2mm ML); Horseshoe Harbour, Mawson Station [67°40'S, 63°00'E], ANARE, 10 Mar 1960, NMV F22851 (mature ♀, 52.8mm ML); 67°18'S, 65°34'E, 110m, ANARE, 3 Dec 1982, NMV F65690 (submature ♀, 26.5mm ML); 67°07'S, 70°17'E, 256m, ANARE, 2 Feb 1986, NMV F65691 (mature ♂, 47.7mm ML).

Off Amery Ice Shelf, Prydz Bay: 67°19'S, 71°25'E, 562–567m, MS *Nella Dan*, Stn Prydz-87-27, ANARE, T. G. Cochran, 22 Feb 1987, NMV F65693 (submature ♀, 36.0mm ML); 66°48'S, 72°33'E, 526–532m, RSV *Aurora Australis*, Stn AA91-89(2), ANARE, C. C. Lu and T. N. Stranks, 24 Feb 1991, NMV F67885 (immature ♂, 29.2 and 34.6mm ML);

68°03'S, 73°13'E, 680–683 m, RSV *Aurora Australis*, Stn AA91-84, ANARE, C. C. Lu and T. N. Stranks, 21 Feb 1991, NMV F65698 (mature ♀, 64.5 mm ML); 68°26'S, 75°24'E, 616–622 m, RSV *Aurora Australis*, Stn AA91-78, ANARE, C. C. Lu and T. N. Stranks, 19 Feb 1991, NMV F65695 (mature ♂, 52.7 mm ML); 67°56'S, 76°24'E, 436–441 m, RSV *Aurora Australis*, Stn AA91-77, ANARE, C. C. Lu and T. N. Stranks, 18 Feb 1991, NMV F65697 (mature ♂, 35.5 mm ML); 67°21'S, 77°19'E, 333–341 m, RSV *Aurora Australis*, Stn AA91-75, ANARE, C. C. Lu and T. N. Stranks, 17 Feb 1991, NMV F65696 (submature ♀, 18.7 mm ML; immature ♂, 23.1 mm ML); 67°21'S, 77°20'E, 337–343 m, MS *Nella Dan*, Stn Prydz-87-40, ANARE, T. G. Cochran, 27 Feb 1987, NMV F65694 (mature ♀, 53.3 mm ML), USNM 884247 (mature ♂, 45.7 mm ML); 67°33'S, 77°30'E, 298–301 m, RSV *Aurora Australis*, Stn AA91-76, ANARE, C. C. Lu and T. N. Stranks, 18 Feb 1991, NMV F67888 (submature ♀, 24.7 mm ML; immature ♂, 18.3 mm ML); 67°02'S, 78°15'E, 251–266 m, RSV *Aurora Australis*, Stn AA91-74, ANARE, C. C. Lu and T. N. Stranks, 17 Feb 1991, NMV F67887 (mature ♂, 34.6 mm ML).

Diagnosis. Medium sized animals (ML to 65 mm; TL to 210 mm) (fig. 2); mantle spherical (MWI 83.3–*92.7*–101.2); head moderately wide, narrower than mantle (HWI 55.5–*69.8*–82.6), demarked from mantle by moderate constriction; eyes large, project above surface of head. Funnel large, stout, bluntly tapered (FuLI 35.6–*40.9*–47.6); funnel organ VV-shaped, limbs thick, outer limbs as long as median limbs (fig. 9g). Mantle aperture very wide (PAI 80.9–*100.6*–122.2). Arms short (MAI 48.1–*57.3*–74.2) (1.5–2.3 times ML in mature animals), stout, tapering to fine tips. Arm lengths subequal, arm order usually 4.3.2.1 (ALI, arm 1: 118.8–*159.3*–187.3; arm 2: 119.6–*166.0*–200.0; arm 3: 129.8–*169.9*–204.2; arm 4: 128.0 –*173.5*–207.8). Arm suckers uniserial, raised from arm surface, small (ASI 4.9–*6.6*–10.9), without sucker enlargement. Third right arm of males hectocotylised, shorter than its opposite number (OAI 87.6–*90.3*–92.4; HcAI 124.7–*158.3*–177.5); ligula medium size, 5–9% of third right arm length in mature animals (LLI 5.0–*6.6*–8.1); ligula groove long, well marked and shallow, without transverse ridges; calamus long, pointed (CaLI 34.8–*47.5*–66.7) (figs 9e, f); hectocotylised arm with 31–38 suckers; opposite arm with 37–54 suckers. Web moderately deep (WDI 23.0–*30.6*–44.8), web formula usually B=C=DAE. Ink sac present. Gill lamellae 7–8. Mature ovarian eggs, from females with enlarged ovaries, large (11–14 mm long, 5–7 mm wide) (EgLI 18.1–*21.1*–23.8; EgWI 7.9–*9.9*–11.4). Male with long penis (PLI 21.7–*37.4*–46.5), with single coiled diverticulum (fig. 9h); spermatophores long (SpLI 55.5–*139.7*–164.5), slender (SpWI 4.0–*4.5*–5.0), with large, coiled sperm reservoir (SpRI 26.4–*30.3*–32.8).

Integumental sculpture consists of pattern of fine, rounded and closely set papillae on dorsal surface; papillae absent from ventral surface. Large unbranched primary papillae present in ocular region, with one supraocular papilla. Ventrolateral integumentary ridge present. In life, colour of resting animals uniformly pink-brown to purple-brown dorsally, cream-white ventrally. When stimulated, animals become darker in colour, dark purple-brown dorsally, cream-white ventrally. Papillae on dorsum usually slightly darker than background, giving spotted appearance. White spots consist of one spot on mid-dorsal brachial crown, and one broad spot on mid-dorsal posterior mantle. White transverse bar present between eyes. Ocelli absent.

Males mature at approximately 35 mm ML. Females attain ovarian maturity at about 55 mm ML.

Distribution. East Antarctica, from off Enderby Land (65°56'S, 50°52'E), off MacRobertson Land (66°59'S to 67°40'S, 62°49'E to 65°34'E), off the Amery Ice Shelf, Prydz Bay (66°48'S to 68°26'S, 71°25'E to 78°15'E) (this study); and off Queen Mary Land (66°08'S, 94°17'E) (Berry, 1917). West Antarctica, from off Graham Land (65°05'S, 63°55'W) (Joubin, 1905). Other distributional records remain to be verified, but the species probably has a circumpolar distribution. The species has been collected on the Antarctic continental shelf at depths ranging from 110–683 m, with temperatures from -2.1 to -1.6°C, on mud and sand bottoms with pebbles and rocks, and among sponges, gorgonaceans and bryozoans.

Remarks. P. charcoti, along with *P. harrissoni* (Berry), are probably the most commonly-occurring eledonines in East Antarctic waters. The present material provides a comprehensive series of life history stages, including mature males and females.

Examination of the type specimen of *P. aurorae* (Berry) allowed us to check Berry's (1918 postscript) suspicion that the species was conspecific with *P. charcoti.* The holotype of *P. aurorae* is an immature male, not a mature animal as Berry (1917) stated. Through dehydration of the type specimen over time, some shrivelling of the arm tips including the hectocotylised arm tip has occurred. Our present study has shown that the morphological counts and measurements for *P. aurorae* fall within the ranges of variation known for *P. charcoti*, and we therefore confirm that the two species are synonymous.

Figure 2. *Pareledone charcoti* (Joubin): a, dorsal, and b, lateral, view of NMV F65695, ♂, 52.7 mm ML.

Pareledone framensis sp. nov.

Figures 3, 4, 9i–l

Material examined. Holotype: Antarctica, off MacRobertson Land, Fram Bank (67°29'S, 68°50'E), 145–150 m, RSV *Aurora Australis*, Stn AA91-100, ANARE, C. C. Lu and T. N. Stranks, 28 Feb 1991, NMV F65665 (mature ♂, 58.9 mm ML) (preserved in ethyl alcohol).

Paratypes: locality as above, AM C173818 (mature ♂, 67.6 mm ML), NMV F65667 (mature ♂, 62.9 mm ML), USNM 884250 (mature ♂, 53.8 mm ML).

Other material examined: Antarctica, off MacRobertson Land, Fram Bank: 67°29'S, 68°50'E, 145–150 m, RSV *Aurora Australis*, Stn AA91-100, ANARE, C. C. Lu and T. N. Stranks, 28 Feb 1991, NMV F65618 (immature ♂, 18.4 mm ML); 67°11'S, 69°15'E, 307–319 m, MS *Nella Dan*, Stn Prydz-87-23, ANARE, T. G. Cochran, 21 Feb 1987, NMV F65619 (submature ♀, 33.4 mm ML; mature ♂, 61.0 mm ML); 67°15'S, 70°06'E, 172–182 m, RSV *Aurora Australis*, Stn AA91-95, ANARE, C. C. Lu and T. N. Stranks, 26 Feb 1991, NMV F65621 (submature ♀, 17.7 mm ML); 67°25'S, 70°20'E, 161–165 m, RSV *Aurora Australis*, Stn AA91-94, ANARE, C. C. Lu and T. N. Stranks, 26 Feb 1991, NMV F65620 (immature ♂, 25.2 mm ML).

Diagnosis. Medium sized animals (ML to 70 mm; TL to 280 mm) (figs 3, 4a); mantle spherical (MWI 80.7–*91.2*–99.6); head moderately wide, narrower than mantle (HWI 52.7–*63.4*–75.0), demarked from mantle by moderate constriction; eyes large, project above surface of head. Funnel large, stout, bluntly tapered (FuLI 35.2–*39.5*–43.5); funnel organ VV-shaped, limbs thick, outer limbs three-quarters as long as median limbs (fig. 9k). Mantle aperture wide (PAI 76.2–*90.0*–106.3). Arms long (MAI 29.0–*34.2*–38.3) (2.7–3.4 times ML in mature animals), stout, tapering to fine tips. Arm lengths subequal, arm order usually 4.3.2.1 (ALI, arm 1: 195.9–*261.3*–312.9; arm 2: 218.0–*265.7*–321.0; arm 3: 227.5–*268.4*–310.0; arm 4: 258.9–*285.4*–345.1). Arm suckers uniserial, raised from arm surface, small (ASI 4.7–*6.5*–9.9), without sucker enlargement. Third right arm of males hectocotylised, shorter than its opposite number (OAI 74.2–*80.5*–91.4; HcAI 178.4–*210.2*–241.8) (fig. 4b); ligula medium size, 5–8% of third right arm length in mature animals (LLI 5.9–*6.4*–7.5); ligula groove long, well marked and shallow, without transverse ridges; calamus long, pointed (CaLI 35.6–*47.9*–56.5) (figs 9i, j); hectocotylised arm with 44–51 suckers; opposite arm with 61–80 suckers. Web shallow (WDI 12.2–*17.4*–22.6), web formula usually DCBAE. Radula with A_{3-5} seriation of the rhachidian (fig. 4f). Ink sac present. Gill lamellae 7–8. Size of mature eggs unknown. Male with long penis (PLI 38.9–*40.9*–43.1), with single coiled diverticulum (fig. 9l); spermatophores long (SpLI 123.2–*138.7*–167.7), slender (SpWI 3.8–*4.5*–5.5), with large, coiled sperm reservoir (SpRI 39.4–*41.7*–43.8).

Integumental sculpture consists of pattern of coarse, rounded and closely set papillae evenly covering dorsum, ventrum, and oral surface of web and lateral surfaces of arms. Large unbranched primary papillae present in ocular region, with one very large supraocular papilla, and on dorsal mantle with four papillae in diamond pattern. Ventrolateral integumentary ridge absent. In life, colour of resting animals uniformly yellow-brown to gold dorsally, white to cream-white ventrally. When stimulated, animals become darker in colour, uniformly golden-brown dorsally, and yellow-brown ventrally. White spots consist of one spot on lateral head, just ventral to each eye; and streak on the lateral mantle, posterior to each eye. White transverse bar present between eyes. Dorsal mantle and frontal white spots absent. Lateral head white spots and head bar conspicuous in live animals, often faded and inconspicuous in preserved animals. Ocelli absent.

Males mature at approximately 50–55 mm ML. No mature females were encountered.

Distribution. Known only from Fram Bank, off MacRobertson Land, East Antarctica (67°11'S to 67°29'S, 68°50'E to 70°20'E). An inshore species collected at depths ranging from 145–319 m, with temperatures from -2.2 to -2.1°C, on mud bottom with pebbles and rocks, and among sponges and ascidians.

Etymology. Named after the type locality, Fram Bank.

Remarks. This new species can be distinguished from all other valid congeners of *Pareledone* (listed in Table 1) by, among other characters, coarse papillation over the entire surface, and the colour pattern of gold with white spots and streaks. Additionally, this species can be distinguished from *P. adelieana* (Berry, 1917) by the narrower head width, the longer relative arm length, a higher sucker count on the hectocotylised arm (HASC) and opposite arm (OASC), the shorter ligula length index, the ligula groove without transverse ridges, and a VV- rather than W-shaped funnel organ. *P. framensis* also differs from *P. charcoti* (Joubin, 1905) by the longer relative arm length, a higher HASC and OASC, and the lack of a ventrolateral

Figure 3. *Pareledone framensis* sp. nov.: a, dorsal, and b, lateral, view of USNM 884250, paratype, ♂, 53.8 mm ML.

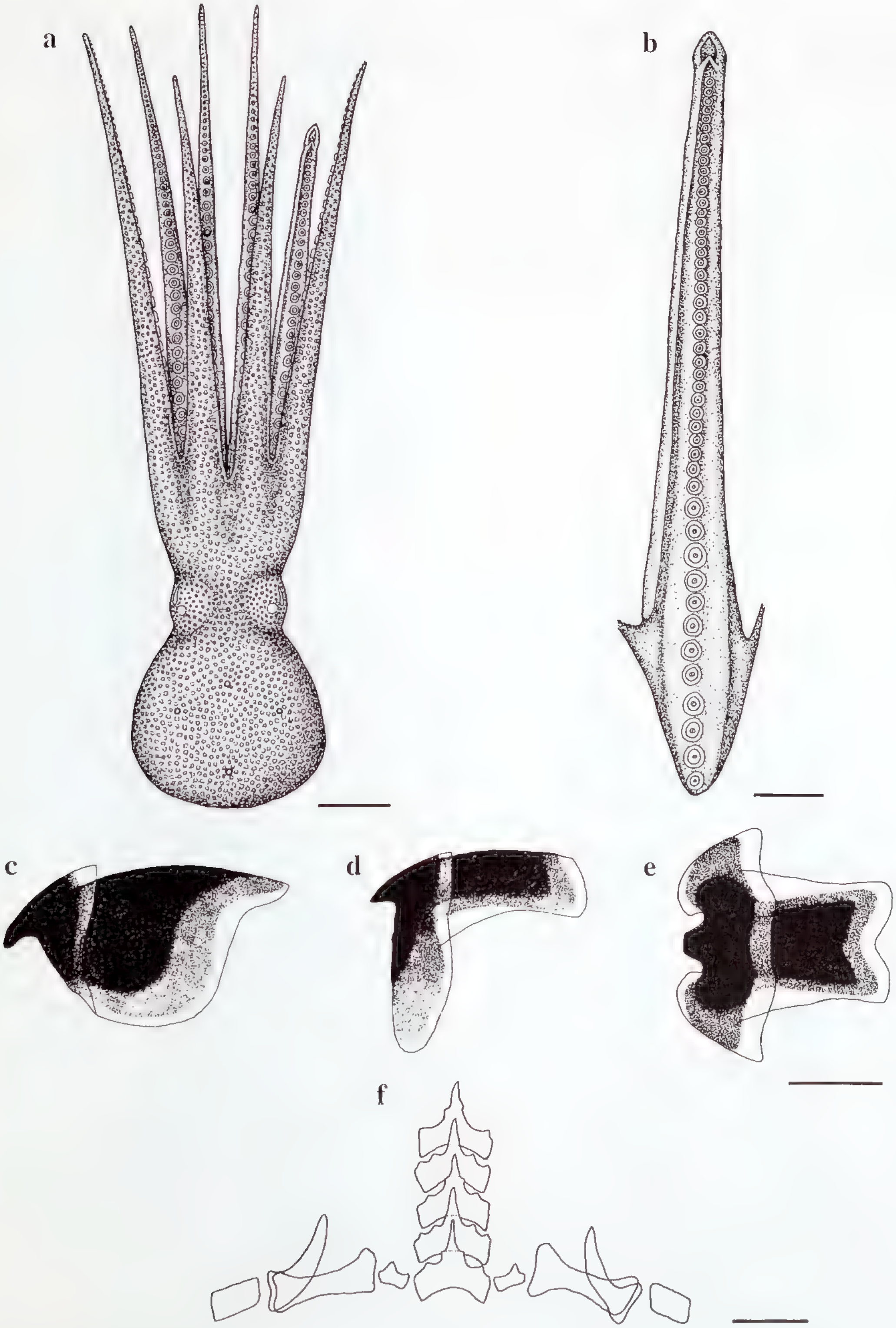

Figure 4. *Pareledone framensis* sp. nov.: a, dorsal view of holotype, NMV F65665, ♂, 58.9 mm ML (scale bar = 20 mm); b, hectocotylised arm of NMV F65619, 61.0 mm ML (scale bar = 10 mm); c, upper beak, d and e, lower beak (scale bar = 2 mm), and f, radula (scale bar = 0.5 mm), of paratype, AM C173818, ♂, 67.6 mm ML.

integumentary ridge. It also differs from *P. harrissoni* (Berry, 1917) by having a narrower head width (see fig. 9; Tables 2, 3).

P. framensis can be distinguished easily from other eledonine species by a combined suite of characters including: a broadly ovoid mantle; skin with a characteristic pattern of coarse papillation on the dorsal, ventral and oral surfaces, but no ventrolateral ridge; large and prominent eyes; long, subequal arms (2.7–3.4 times ML in mature animals); small suckers; a shallow web (12–23% of arm length); a medium sized ligula (5–8% of third right arm length in mature animals), and 7–8 gill lamellae.

Pareledone harrissoni (Berry)

Figures 5, 9m–p

Moschites harrissoni Berry, 1917: 24, text figs 21–25, pl. 13 fig. 13, pl. 14 figs 14–16.

[?]*Moschites antarcticus* Thiele, 1920: 434, pl. 52 figs 1, 2.

Pareledone harrissoni. — Robson, 1932: 277. — ?Dell, 1959: 92, text figs 1–3.

[?]*Pareledone antarctica*. — Robson, 1932: 279.

Pareledone harrisoni [*sic*]. — Voss, 1988: 300 [designation of *nomen dubium*].

Material examined. Holotype: Antarctica, off Shackleton Ice Shelf (65°06'S, 96°13'E), 325 fm [595 m], SY *Aurora*, Stn 10, Australasian Antarctic Expedition, 29 Jan 1914, AM C40892 (submature ♀, 53.8 mm ML).

Paratypes: Antarctica, 'Western Base' [66°20'S, 95°00'E], 270 fm [494 m], Australasian Antarctic Expedition, Jan 1913, AM C40893 (submature ♀, 62.2 mm ML); off Shackleton Ice Shelf (66°44'S, 97°28'E), 358 fm [654 m], SY *Aurora*, Stn 11, Australasian Antarctic Expedition, 31 Jan 1914, USNM 815724 (♀, 54 mm ML, not seen).

Other material examined: Antarctica, off MacRobertson Land: 66°59'S, 62°49'E, 117 m, ANARE, 6 Feb 1986, NMV F65678 (submature ♀, 74.5 mm ML); 67°18'S, 65°34'E, 110 m, ANARE, 3 Dec 1982, NMV F65679 (submature ♀, 23.2 and 59.7 mm ML); 67°29'S, 68°50'E, 145–150 m, RSV *Aurora Australis*, Stn AA91-100, ANARE, C. C. Lu and T. N. Stranks, 28 Feb 1991, NMV F65680 (mature ♂, 91.6 mm ML); 67°15'S, 68°56'E, 139 m, RSV *Aurora Australis*, Stn AA91-99, ANARE, C. C. Lu and T. N. Stranks, 28 Feb 1991, USNM 884251 (mature ♂, 70.7 mm ML).

Off Amery Ice Shelf, Prydz Bay: 68°00'S, 71°18'E, 515–523 m, MS *Nella Dan*, Stn Prydz-87-20, ANARE, T. G. Cochran, 20 Feb 1987, NMV F65682 (submature ♀, 37.1 and 45.2 mm ML); 66°48'S, 72°33'E, 526–532 m, RSV *Aurora Australis*, Stn AA91-89(2), ANARE, C. C. Lu and T. N. Stranks, 24 Feb 1991, NMV F65615 (submature ♀, 61.1 mm ML; immature ♂, 33.5 mm ML); 66°46'S, 72°37'E, 530 m, RSV *Aurora Australis*, Stn AA91-89, ANARE, C. C. Lu and T. N. Stranks, 24 Feb 1991, NMV F65687 (immature ♂, 20.0 mm ML); 68°30'S, 73°14'E, 743 m, RSV *Aurora Australis*, Stn AA91-80, ANARE, C. C. Lu and T. N. Stranks, 20 Feb 1991, NMV F67886 (submature ♀, 27.5 and 47.6 mm ML; immature ♂, 27.9 mm ML); 66°48'S, 73°31'E, 696–732 m, MS *Nella Dan*, Stn Prydz-87-30, ANARE, T. G. Cochran, 24 Feb 1987, NMV F65683 (mature ♂, 57.3 mm ML); 67°25'S, 74°34'E, 460 m, ANARE, 26 Jan 1986, NMV F65681 (mature ♂, 84.9 mm ML); 67°00'S, 75°01'E, 385–388 m, RSV *Aurora Australis*, Stn AA91-86, ANARE, C. C. Lu and T. N. Stranks, 22 Feb 1991, NMV F67890 (submature ♀, 20.6 and 31.8 mm ML; immature ♂, 23.8 mm ML); 68°26'S, 75°24'E, 616–622 m, RSV *Aurora Australis*, Stn AA91-78, ANARE, C. C. Lu and T. N. Stranks, 19 Feb 1991, NMV F65686 (submature ♀, 35.0 mm ML); 67°01'S, 76°25'E, 327–332 m, RSV *Aurora Australis*, Stn AA91-85, ANARE, C. C. Lu and T. N. Stranks, 22 Feb 1991, NMV F67889 (submature ♀, 24.8 mm ML); 67°21'S, 77°20'E, 337–343 m, MS *Nella Dan*, Stn Prydz-87-40, ANARE, T. G. Cochran, 27 Feb 1987, NMV F65685 (mature ♀, 99.5 mm ML); 67°11'S, 78°16'E, 188–208 m, MS *Nella Dan*, Stn Prydz-87-31, ANARE, T. G. Cochran, 25 Feb 1987, NMV F65684 (submature ♀, 76.3 mm ML).

Diagnosis. Medium sized animals (ML to 100 mm; TL to 350 mm) (fig. 5); mantle spherical to ovoid (MWI 73.6–*88.2*–100.3); head moderately wide, slightly narrower than mantle (HWI 51.9–*72.9*–91.0), demarked from mantle by moderate constriction; eyes large, project above surface of head. Funnel large, stout, bluntly tapered (FuLI 26.2–*35.8*–44.5); funnel organ VV-shaped, limbs thick, outer limbs as long as median limbs (fig. 9o). Mantle aperture wide (PAI 72.6–*99.5*–114.6). Arms long (MAI 29.9–*44.8*–56.0) (1.8–3.6 times ML in mature animals), stout, tapering to fine tips. Arm lengths subequal, arm order usually 4.3.2.1 (ALI, arm 1: 168.5–*205.6*–289.7; arm 2: 169.7–*213.1*–321.8; arm 3: 175.9–*216.8*–334.5; arm 4: 170.2–*221.4*–329.1). Arm suckers uniserial, raised from arm surface, small (ASI 5.1–*7.5*–10.3), without sucker enlargement. Third right arm of males hectocotylised, shorter than its opposite number (OAI 77.6–*85.6*–89.0; HcAI 181.2–*211.2*–259.5); ligula small, 4–11% of third right arm length in mature animals (LLI 4.7–*6.5*–10.1); ligula groove long, well marked and shallow, without transverse ridges; calamus long, pointed (CaLI 31.4–*43.3*–56.4) (figs 9m, n); hectocotylised arm with 36–50 suckers; opposite arm with 37–79 suckers. Web moderately deep (WDI 21.5–*24.5*–32.1), web formula usually B=C=DAE. Ink sac present. Gill lamellae 8–9. Mature ovarian eggs, from female with enlarged ovary, large (12–14 mm long, 6–7 mm wide) (EgLI 12.6–*13.5*–14.3; EgWI 6.3–*6.7*–7.0). Male with long penis (PLI 11.9–*35.7*–44.5), with single coiled diverticulum (fig. 9p); spermatophores long (SpLI 70.1–*118.1*–141.4), slender (SpWI 3.8–*4.7*–6.2), with large, coiled sperm reservoir (SpRI 38.5–*44.8*–51.3).

Figure 5. *Pareledone harrissoni* (Berry): a, dorsal, and b, lateral, view of USNM 884251, ♂, 70.7 mm ML.

Integument loose and wrinkled, sometimes with gelatinous consistency. Integumental sculpture consists of pattern of fine, rounded and widely scattered papillae on dorsal surface; papillae absent from ventral surface. Large unbranched primary papillae present in ocular region, with one large supraocular papilla. Ventrolateral integumentary ridge absent. In life, colour of resting animals uniformly pink to purple–pink dorsally, cream–white to pale pink ventrally. When stimulated, animals become darker in colour, uniformly brown–pink to brown–purple dorsally, purple–pink ventrally. White spots consist of one spot on mid-dorsal brachial crown. White transverse bar present between eyes. Ocelli absent.

Males mature at approximately 50 mm ML. Females attain ovarian maturity at about 90 mm ML.

Distribution. East Antarctica, from off MacRobertson Land (66°59'S to 67°29'S, 62°49'E to 68°56'E), off the Amery Ice Shelf, Prydz Bay (66°46'S to 68°30'S, 71°18'E to 78°16'E) (this study); and off the Shackleton Ice Shelf (65°06'S to 66°44'S, 95°00'E to 97°28'E) (Berry, 1917). Other distributional records remain to be verified, but the species is probably restricted in distribution to East Antarctic waters. The species has been collected on the Antarctic continental shelf at depths ranging from 25–743 m, with temperatures from -2.1 to -0.6°C, on mud and sand bottoms with pebbles and rocks, and among sponges, gorgonaceans and bryozoans.

Remarks. Apart from *Megaleledone senoi*, *Pareledone harrissoni* is the largest eledonine occurring in East Antarctic waters. The present material, comprises a comprehensive growth series from smaller juveniles to mature males and females. The morphology of the species is somewhat variable in terms of mantle shape, mantle length relative to arm length, and sucker count (e.g. the specimen in fig. 5, USNM 884251, has a relatively low mantle–arm index), although in some cases the variation may be an artefact of preservation techniques.

Voss (1988) designated *P. harrissoni* (Berry) as a *nomen dubium*, but reasons for his decision were not given, nor is it clear whether he personally examined the type specimens. Type material of *P. harrissoni* was examined for this study and although two of the specimens are in a deteriorated condition, the species does have valid characters that may be assessed.

Robson (1932) postulated that *P. antarctica* (Thiele) was the same species as *P. harrissoni*. The type material of *P. antarctica* was not available for examination, but comparison of the type description and illustrations of *P. antarctica* by Thiele (1920) with the present material suggests that the species is conspecific with *P. harrissoni*. *P. antarctica* is thus a probable junior synonym of *P. harrissoni*.

Pareledone prydzensis sp. nov.

Figures 6, 7, 9q–t

Material examined. Holotype: Antarctica, off Amery Ice Shelf, Prydz Bay (66°48'S, 72°33'E), 526–532 m, RSV *Aurora Australis*, Stn AA91-89(2), ANARE, C. C. Lu and T. N. Stranks, 24 Feb 1991, NMV F65666 (mature ♂, 29.4 mm ML) (preserved in ethyl alcohol).

Paratypes: locality as above, AM C173819 (submature ♀, 25.7 mm ML), NMV F65625 (submature ♀, 20.7 mm ML; mature ♂, 28.2 mm ML), USNM 884249 (mature ♂, 25.8 mm ML).

Other material examined: Antarctica, off Amery Ice Shelf, Prydz Bay: 66°42'S, 71°56'E, 667–676 m, RSV *Aurora Australis*, Stn AA91-92, ANARE, C. C. Lu and T. N. Stranks, 25 Feb 1991, NMV F65614 (immature ♂, 20.9 mm ML); 66°46'S, 72°37'E, 530 m, RSV *Aurora Australis*, Stn AA91-89, ANARE, C. C. Lu and T. N. Stranks, 24 Feb 1991, NMV F65624 (submature ♀, 15.0 mm ML).

Diagnosis. Small animals (ML to 30 mm; TL to 95 mm) (figs 6, 7a); mantle spherical (MWI 78.0–*94.0*–102.7); head wide, slightly narrower than mantle (HWI 80.4–*83.9*–87.4), demarked from mantle by slight constriction; eyes large, do not project far above surface of head. Funnel large, stout, bluntly tapered (FuLI 41.3–*46.7*–51.4); funnel organ VV-shaped, limbs thick, outer limbs three-quarters as long as median limbs (fig. 9s). Mantle aperture very wide (PAI 83.7–*106.3*–122.2). Arms short (MAI 51.7–*58.6*–69.4) (1.9–2.3 times ML in mature animals), stout, tapering to narrow tips. Arm lengths subequal, arm order 4=3=2.1 (ALI, arm 1: 134.6–*160.0*–179.1; arm 2: 140.7–*163.5*–193.3; arm 3: 138.0–*163.8*–180.1; arm 4: 137.3–*166.6*–180.9). Arm suckers uniserial, raised from arm surface, small (ASI 6.0–*6.8*–7.7), without sucker enlargement. Third right arm of males hectocotylised, slightly shorter than its opposite number (OAI 90.7–*94.9*–102.0; HcAI 155.4–*160.1*–169.5) (fig. 7b); ligula medium size, 6–9% of third right arm in mature animals (LLI 6.5–*7.5*–8.2); ligula groove long, well marked and shallow, without transverse ridges; calamus long, pointed (CaLI 48.5–*52.0*–54.8) (figs 9q, r); hectocotylised arm with 26–29 suckers; opposite arm with 29–36 suckers. Web deep (43.5–*47.4*–51.1), web formula usually B=C=DAE. Radula with A_{2-3} seri-

ation of the rhachidian (fig. 7f). Ink sac present. Gill lamellae 6–7. Size of mature eggs unknown. Male with long penis (PLI 39.4–*41.1*–43.9), with single coiled diverticu-lum (fig. 9t); spermatophores long (SpLI 119.9–*123.6*–130.6), slender (SpWI 6.0–*6.1*–6.2), with large, coiled sperm reservoir (SpRI 27.1–*30.4*–34.3).

Integumental sculpture consists of pattern of fine, rounded and closely set papillae on dorsal surface; ventral surface smooth; no larger papillae appear to be present in ocular region or on dorsal mantle. Ventrolateral integumentary ridge present. In life, colour of resting animals grey–purple to pink–purple on the dorsal mantle and head; darker pink–purple on dorsal brachial crown, web and arms; and cream–white to pink–white ventrally. When stimulated, animals become darker in colour, dark purple–pink on dorsal mantle and head; dark purple–brown to black on dorsal brachial crown, web and arms; and light pink–purple ventrally. White spots consist of one spot on mid-dorsal brachial crown, and one broad spot on mid-dorsal posterior mantle. White transverse bar present between eyes. Ocelli absent.

Males mature at approximately 25 mm ML. No mature females were encountered.

Distribution. Known only from Prydz Bay, off the Amery Ice Shelf, East Antarctica (66°42'S to 66°48'S, 71°56'E to 72°37'E). An inshore species collected at depths ranging from 526–676 m, with temperatures from -2.1 to -0.6°C, on mud and sand bottoms with rocks, and among sponges and gorgonaceans.

Etymology. Named after the type locality, Prydz Bay.

Remarks. This new species can be readily distinguished from the other valid species of *Pareledone* recognised in this paper (see Table 1). It can be distinguished from *P. charcoti* by its smaller absolute size at maturity, the much deeper web comprising about 45% of arm length, and the striking colour pattern of the very dark brachial crown, web and arms. *P. prydzensis* also differs from *P. adelieana* by having the head narrower rather than wider than the mantle, the shorter ligula length index, the ligula groove without transverse ridges, the VV- rather than W-shaped funnel organ, a differently shaped penis, and a papillate rather than smooth integument. It can also be distinguished from *P. harrissoni* by the lower gill count, and papillate rather than smooth integumental sculpture. *P. prydzensis* may also be distinguished from the other new species described above, *P. framensis*, by a relatively wider head, the shorter relative arm length, and a lower hectocotylised arm sucker count and opposite arm sucker count (see fig. 9, Tables 2, 3).

P. prydzensis can be easily distinguished from other eledonine species on the basis of a combination of characters: a broadly ovoid mantle; skin with a characteristic pattern of fine papillae on the dorsum, and a ventrolateral integumentary ridge; large but not prominent eyes; short, subequal arms (1.9–2.3 times ML in mature animals); small suckers; a deep web (43–51% of arm length); a medium sized ligula (6–9% of third right arm length in mature animals); and 6–7 gill lamellae.

Megaleledone Taki, 1961

Type species. Megaleledone senoi Taki, 1961.

Diagnosis. Benthic octopodids. Mantle saccular, without fins. Eight arms lacking cirri, arms with large uniserial suckers, third right arm of males hectocotylised with end of arm clearly differentiated into ligula and calamus, arms tips not otherwise modified. Web very deep and well developed. Funnel organ VV-shaped. Gills well developed, with 10–11 lamellae. Ink sac present. Crop absent. Radula reduced, with unicuspid rhachidian and lateral teeth present, and marginal plates absent.

Megaleledone senoi Taki

Figures 8, 9u–x

Megaleledone senoi Taki, 1961: 297, text figs 1–8, 16, pls 1, 2. — Kubodera and Okutani, 1986: 133, text fig. 2, pl. 2.

Material examined. Antarctica, off Amery Ice Shelf, Prydz Bay: 66°48'S, 72°33'E, 526–532 m, RSV *Aurora Australis*, Stn AA91-89(2), ANARE, C. C. Lu and T. N. Stranks, 24 Feb 1991, NMV F65529 (submature ♀, 23.6 mm ML); 68°50'S, 73°23'E, 748–761 m, MS *Nella Dan*, Stn Prydz-87-16, ANARE, T. G. Cochran, 20 Feb 1987, NMV F65527 (submature ♀, 131.0 mm ML); 67°19'S, 74°16'E, 464–465 m, MS *Nella Dan*, Stn Prydz-87-47, ANARE, T. G. Cochran, 28 Feb 1987, NMV F65528 (mature ♀, 234.0 mm ML); 67°00'S, 74°23'E, 431–439 m, RSV *Aurora Australis*, Stn AA91-87, ANARE, C. C. Lu and T. N. Stranks, 23 Feb 1991, NMV F60488 (mature ♂, 207.0 mm ML); 67°25'S, 74°34'E, 460 m, ANARE, 26 Jan 1986, NMV F65699 (submature ♀, 30.9 mm ML); 67°00'S, 75°01'E, 385–388 m, RSV *Aurora Australis*, Stn AA91-86, ANARE, C. C. Lu and T. N. Stranks, 22 Feb 1991, NMV F60487 (immature ♂, 169.0 mm ML); 67°54'S, 76°37'E, 431 m, MS *Nella Dan*, Stn Prydz-87-2, ANARE, T. G. Cochran, 16 Feb 1987, NMV F65526 (submature ♀, 181.0 mm ML); 67°21'S, 77°19'E, 333–341 m, RSV *Aurora*

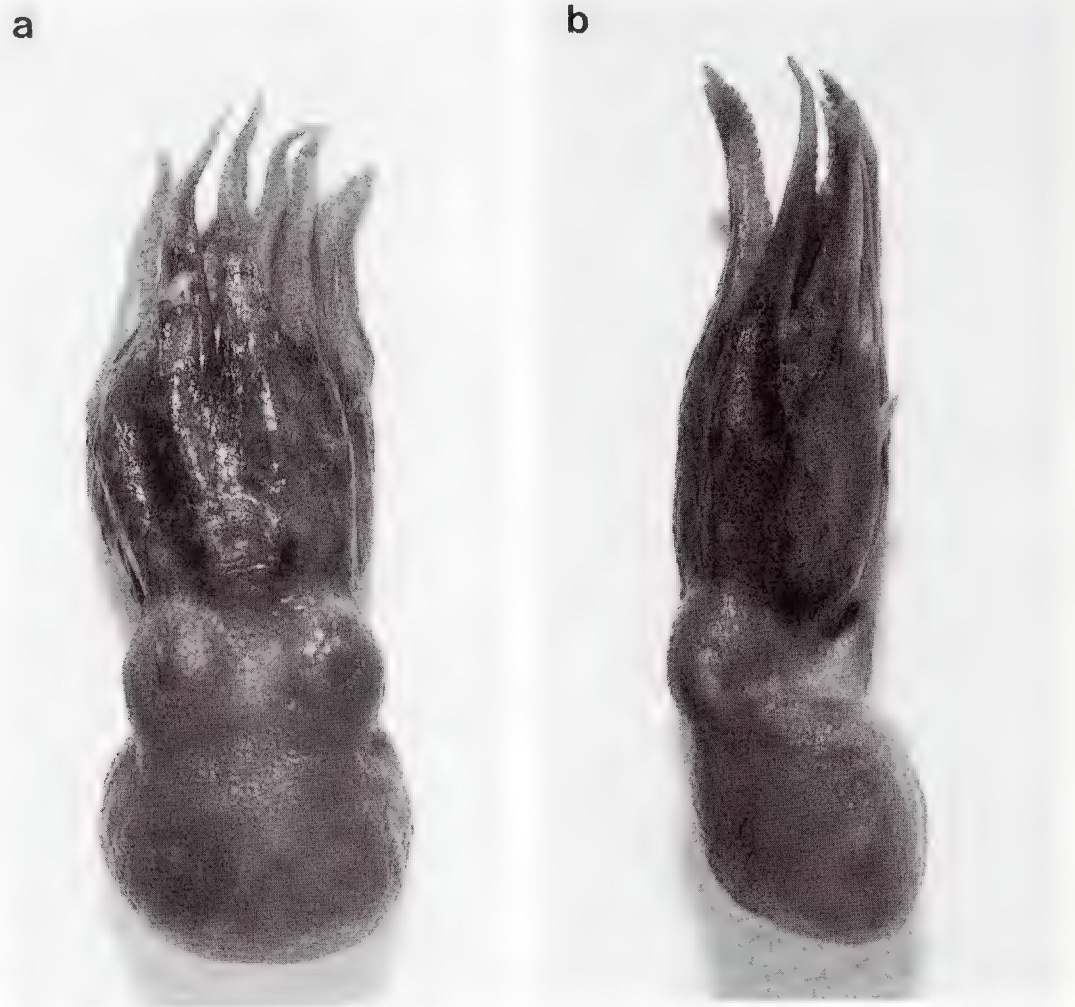

Figure 6. *Pareledone prydzensis* sp. nov.: a, dorsal, and b, lateral, view of NMV F65666, holotype, ♂, 29.4mm ML.

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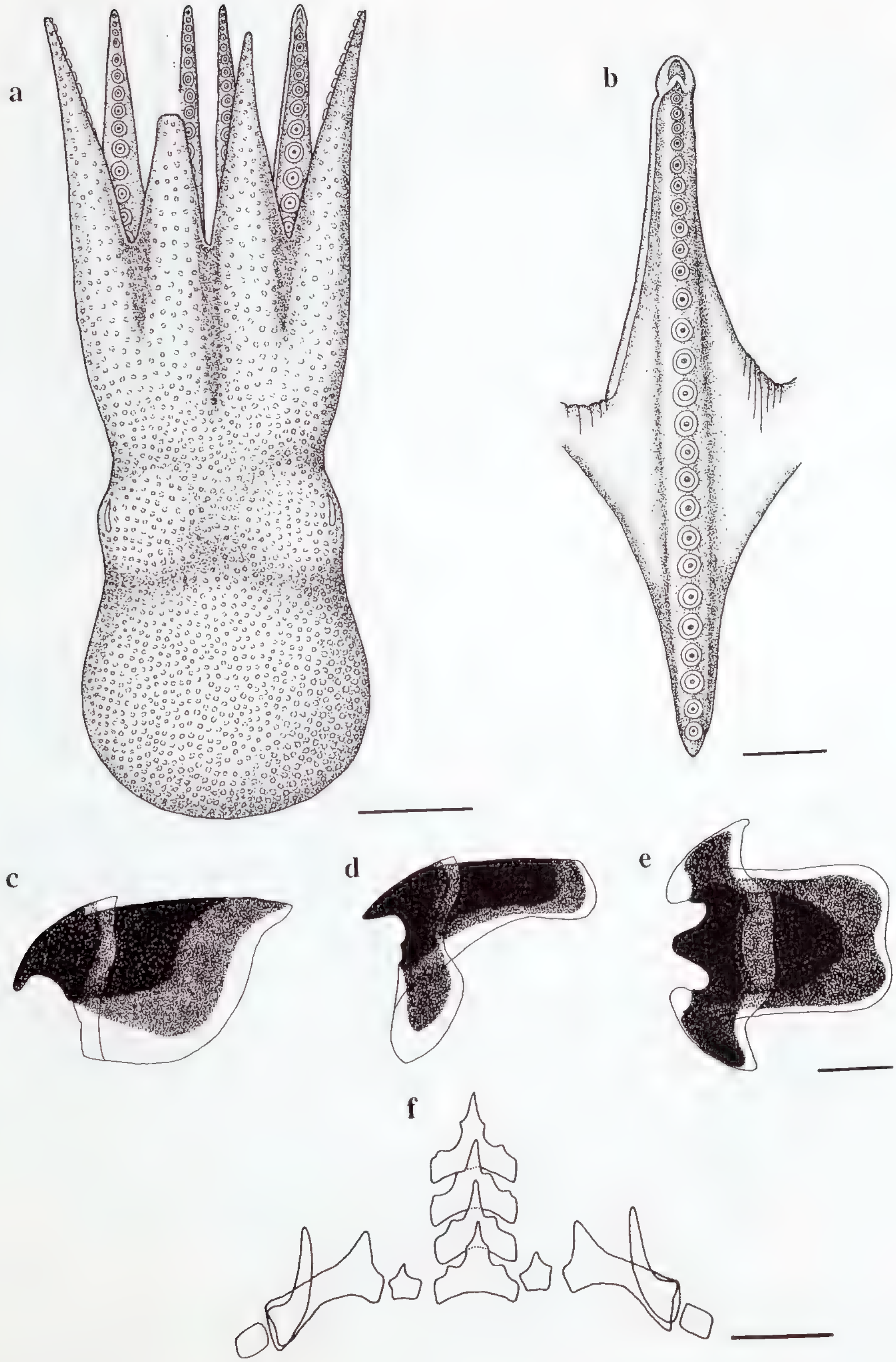
Figure 7. *Pareledone prydzensis* sp. nov.: a, dorsal view (scale bar = 10mm), and b, hectocotylised arm (scale bar = 5mm), of paratype, USNM 884249, 25.8mm ML; c, upper beak, d and e, lower beak, of paratype, NMV F65625, ♂, 28.2mm ML (scale bar = 2mm); and f, radula of NMV F65614, ♂, 20.9mm ML (scale bar = 0.2mm).


a
b
c
d
e
f

Australis, Stn AA91-75, ANARE, C. C. Lu and T. N. Stranks, 17 Feb 1991, NMV F65530 (submature ♀, 44.7, 47.6 and 48.8 mm ML; immature ♂, 42.4 mm ML).

Diagnosis. Large animals (ML to 235 mm; TL to 750 mm) (fig. 8); mantle spherical (MWI 76.0–*96.8*–106.8); head moderately wide, narrower than mantle (HWI 50.0–*65.7*–78.0), demarked from mantle by moderate constriction; eyes small, do not project far above surface of head. Funnel large, stout, bluntly tapered (FuLI 33.8–*38.8*–43.6); funnel organ VV-shaped, limbs thick, outer limbs as long as median limbs (fig. 9w). Mantle aperture very wide (PAI 86.3–*119.8*–144.3). Arms short (MAI 35.3–*41.0*–45.7) (2.0–2.6 times ML in mature animals), stout, tapering to narrow tips. Arm lengths subequal, arm order 4=3=2.1 (ALI, arm 1: 188.9–*219.7*–245.8; arm 2: 195.7–*229.6*–260.9; arm 3: 198.3–*228.4*–260.6; arm 4: 204.3–*236.1*–283.1). Arm suckers uniserial, raised from arm surface, moderately large (ASI 5.9–*8.7*–18.6), without sucker enlargement. Third right arm of males hectocotylised, slightly shorter than its opposite number (OAI 91.2–*92.6*–94.0; HcAI 199.1–*220.5*–259.4); ligula small, 3–4% of third right arm length in mature animals (LLI 3.6); ligula groove long, well marked and shallow, with approximately 10 transverse ridges; calamus long, pointed (CaLI 42.7) (figs 9u, v); hectocotylised arm with 38–40 suckers; opposite arm with 40–69 suckers. Web deep (WDI 40.5–*42.7*–45.3), web formula usually DCBAE. Ink sac present. Gill lamellae 10–11. Mature ovarian eggs, from female with enlarged ovary, large (18–19 mm long; 7–8 mm wide) (EgLI 7.7–*7.9*–8.0; EgWI 3.0–*3.1*–3.2). Males with moderately long penis (PLI 14.7), with single coiled diverticulum (fig. 9x); spermatophore moderately long (SpLI 94.0), slender (SpWI 4.4), with large, coiled sperm reservoir (SpRI 41.4).

Integument thick, loose, wrinkled, with gelatinous consistency. Integumental sculpture consists of pattern of fine, rounded and widely scattered papillae on dorsal surface; papillae absent on ventral surface; no larger papillae in ocular region. Ventrolateral integumentary ridge present. In life, colour of resting animals cream–pink to grey–pink mottled with red–pink patches, and cream–white to pink–white ventrally. When stimulated, animals become darker in colour, dark purple–pink dorsally and light purple–pink ventrally. White spots or bars absent. Ocelli absent.

Males mature at approximately 200 mm ML. Females attain ovarian maturity at about 230 mm ML.

Type. Holotype, female, 135 mm ML. The specimen has not been located, but may be extant in the Taki family collection, Kyoto, Japan (T. Kubodera, National Science Museum, Tokyo, pers. comm.).

Type locality. Antarctica, off Dronning Maud Land (67°51.5'S, 33°13.5'E), 630–680 m.

Distribution. East Antarctica, from off the Amery Ice Shelf, Prydz Bay (66°48'S to 68°50'S, 72°33'E to 77°19'E) (this study); and from the type locality. West Antarctica, from off the Antarctic Peninsula (61°10'S, 55°55'W) (Kubodera and Okutani, 1986). This species appears to have a circumpolar distribution. The species has been collected on the Antarctic continental shelf at depths ranging from 120–761 m, with temperatures from -1.9 to -1.4°C, on mud and sand bottoms with pebbles and rocks, and among sponges and bryozoans.

Remarks. This collection consists of a large number of specimens of *M. senoi*, from immature to mature male and female specimens. Taki (1961) and Nesis and Propp (1968) reported on mature female specimens, but mature males have not been previously described. The large size of the species clearly sets it apart from the other Antarctic eledonids.

The present material from Prydz Bay does not differ from those specimens described by Taki (1961) or Kubodera and Okutani (1986). Taki (1961) noted the resemblance of *M. senoi* to *Graneledone*(?) *setebos* Robson, 1932. The latter species is known only from a "single very mangled and decayed specimen" (Robson, 1932: 313), and has not been well diagnosed to date. The holotype from the BMNH collection has not been available for this study, and the validity of the species cannot be presently determined. If *G. setebos* can be adequately characterised, and is found to be conspecific with *Megaleledone senoi*, there are implications for the correct name of the present species as the former name will have priority over Taki's *senoi*.

The diagnostic features of *Megaleledone* (particularly the broad mantle, narrow head, short arms, deep web, high number of gill lamellae, ribbed ligula groove, and absence of crop) distinguish the genus from *Pareledone*. There does not appear to be any good basis for synonymising *Megaleledone* with *Pareledone*, as

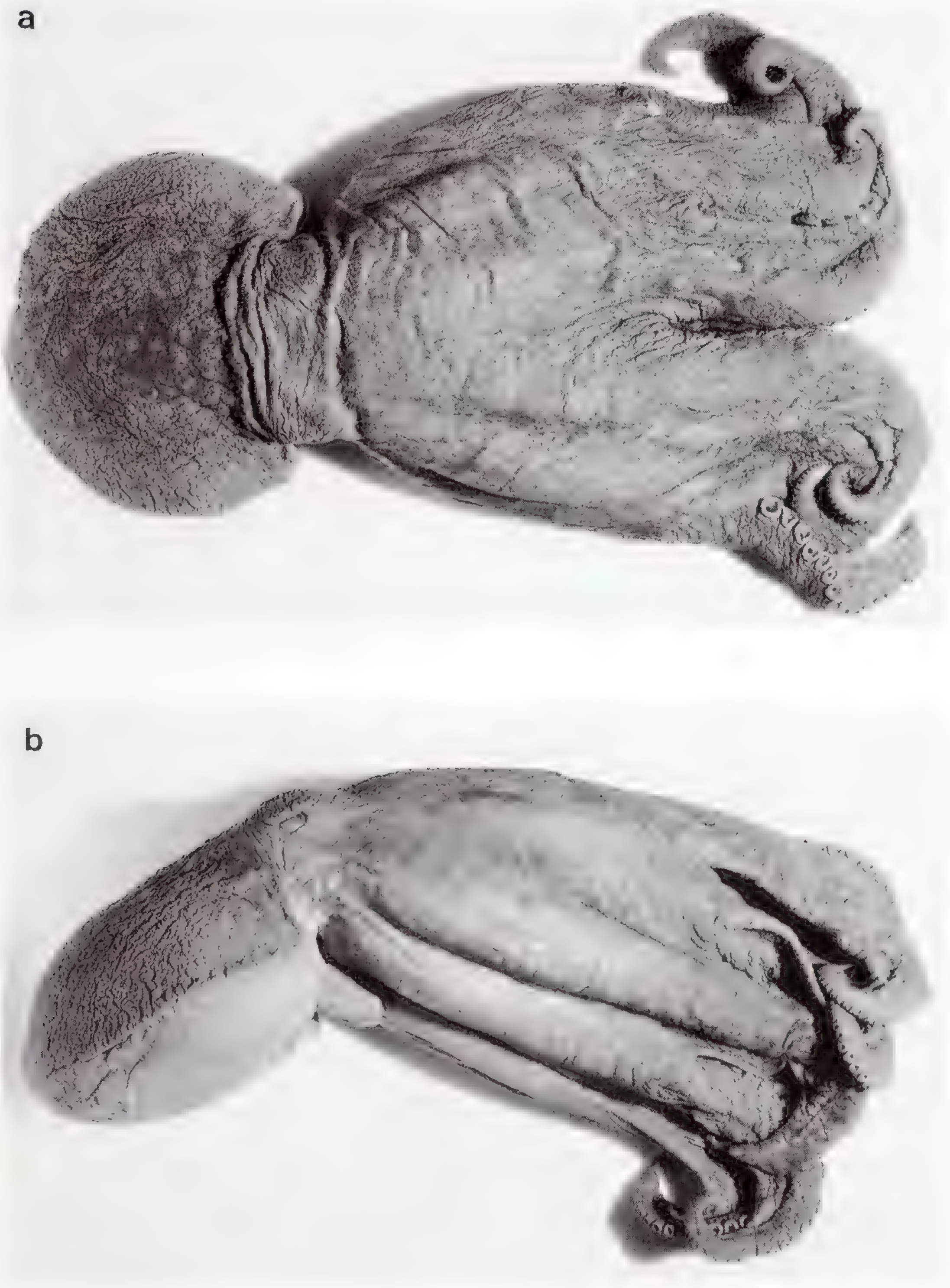
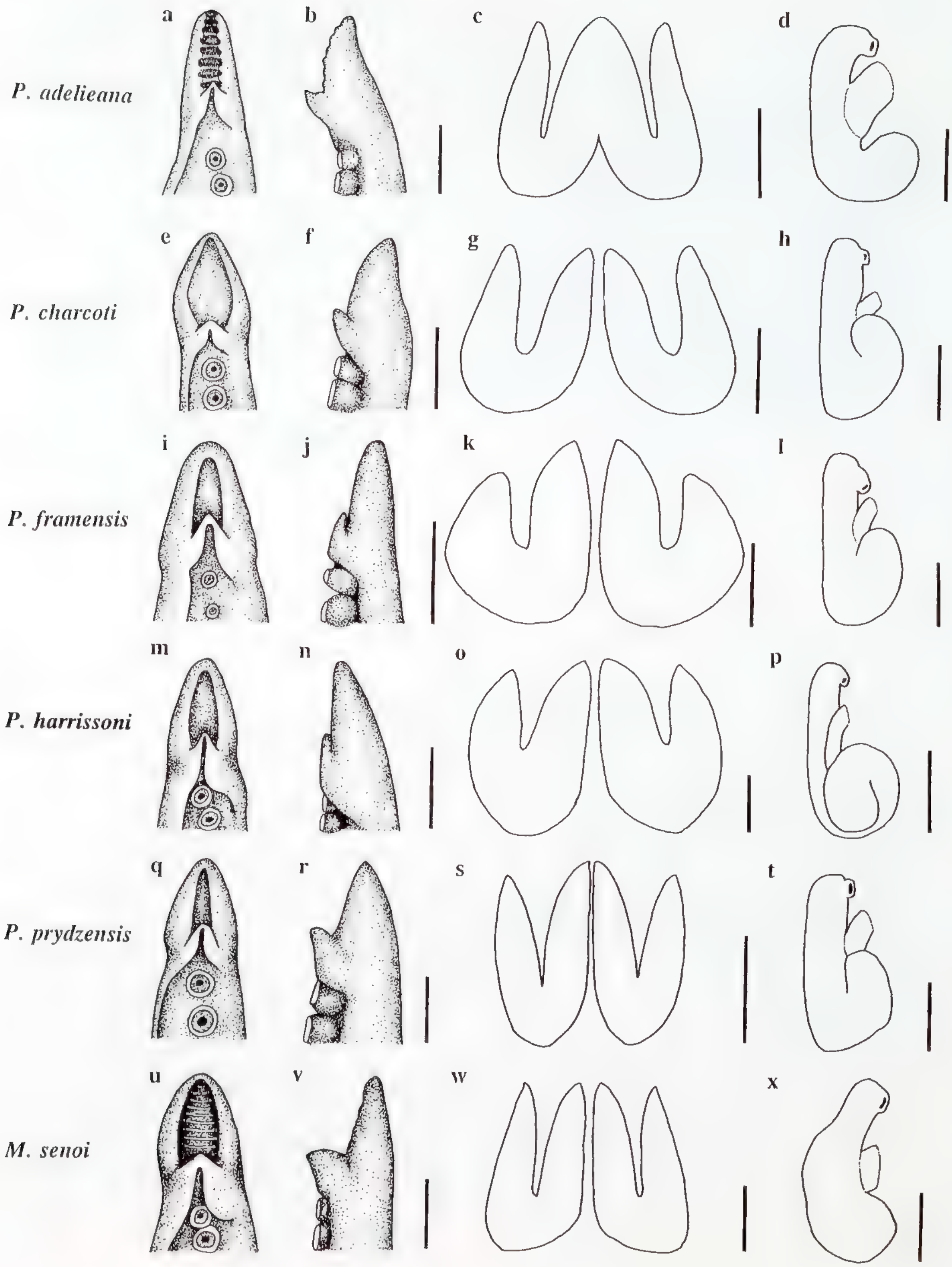


Figure 8. *Megaleledone senoi* Taki: a, dorsal, and b, lateral, view of NMV F60487, ♂, 169.0mm ML.


a b c d
P. adelieana
e f g h
P. charcoti
i j k l
P. framensis
m n o p
P. harrissoni
q r s t
P. prydzensis
u v w x
M. senoi

suggested by Voss (in a personal communication to Palacio, 1978: 289).

Discussion

A large series of specimens, including types of species described by Joubin (1905) and Berry (1917) plus mature males of each species from our collection, has facilitated the present study. Live observations of skin and colour patterns on each described species also benefited our investigation.

Among the 12 nominal species of *Pareledone* currently known, 10 are described from the Southern Ocean, and another two are from the Atlantic Ocean. Of the Atlantic species, *P. nigra* (Hoyle, 1910) was originally described from specimens collected at Lüderitz Bay, Namibia (around 27°S, 15°E). Hoyle (1910) originally placed *nigra* in the *Moschites* genus, but Robson (1932) transferred the species to *Pareledone*. The second Atlantic species, *Pareledone carlgreni* Thore, 1945, was originally diagnosed from material collected at Cape Peninsula, Sea Point, Cape Town, South Africa (~34°S, 15°30'E). Both *P. nigra* and *P. carlgreni* are now being systematically reviewed by Roper and Mangold (in prep.) and should properly be placed in the genus *Aphrodoctopus* (C. F. E. Roper, USNM, pers. comm.).

Once the two Atlantic Ocean species are removed from *Pareledone*, the genus may be considered to have only Antarctic and subantarctic representatives. The 10 nominal species of *Pareledone* from the Southern Ocean are listed in Table 1, with recommendations on their taxonomic status. After examination of available relevant type specimens, additional material and existing published descriptions, five valid species are recognised as occurring in Prydz Bay, East Antarctica: *P. adelieana*, *P. charcoti*, *P. framensis*, *P. harrissoni* and *P. prydzensis* (see fig. 9 and Tables 2 and 3 for comparative information). Detailed taxonomic information and full descriptions of these five species, and a key to the species, will be provided with the future publication of a review of the octopods known from the Prydz Bay region.

At an octopod systematics workshop held during the Symposium on Southern Ocean Cephalopods (Cambridge, England, July 1993), two other distinct and separate species of *Pareledone*, *P. polymorpha* and *P. turqueti*, were recognised from West Antarctic waters. These species are not known to occur in waters of East Antarctica.

The present material of *Pareledone* and *Megaleledone* was collected from water depths shallower than 1000 m, corresponding with the outer edge of the continental shelf in the Prydz Bay vicinity. Although the collecting effort in deeper waters has in the past been poor, from the very limited data available it is doubtful that the range of either genus extends onto the deeper continental slope. The species were all distributed on soft sandy mud substrates and variously among sponge, gorgonacean and bryozoan faunal communities, in waters approximately -1 to -2°C in temperature.

The absolute and relative sizes of mature eggs in *Pareledone adelieana*, *P. charcoti*, *P. harrissoni* and *Megaleledone senoi* were large. Mature eggs of *Pareledone framensis* and *P. prydzensis* were not observed, but judging by the egg development seen in ovaries of submature females, we expect these species to also produce large eggs. Accordingly, we predict that each species will have hatchlings with benthic rather than planktonic development, and thus no potential for long range dispersal (i.e. beyond the Antarctic continent). Ideally this hypothesis would be confirmed

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Figure 9. *Pareledone adelieana* Berry: a, oral, and b, lateral, detail of hectocotylus (scale bar = 5 mm), c, funnel organ (scale bar = 5 mm), and d, penis (scale bar = 5 mm), of USNM 884248, 44.8 mm ML. *Pareledone charcoti* (Joubin): e, oral, and f, lateral, detail of hectocotylus (scale bar = 5 mm), g, funnel organ (scale bar = 5 mm), and h, penis (scale bar = 10 mm), of NMV F65695, 52.7 mm ML. *Pareledone framensis* sp. nov.: i, oral, and j, lateral, detail of hectocotylus (scale bar = 5 mm), k, funnel organ (scale bar = 5 mm), and l, penis (scale bar = 10 mm), of holotype, NMV F65665, 58.9 mm ML. *Pareledone harrissoni* (Berry): m, oral, and n, lateral, detail, of hectocotylus (scale bar = 5 mm), o, funnel organ (scale bar = 5 mm), of USNM 884251, 70.7 mm ML; p, penis of NMV F65680, 91.6 mm ML (scale bar = 20 mm). *Pareledone prydzensis* sp. nov.: q, oral, and r, lateral, detail of hectocotylus (scale bar = 2 mm), s, funnel organ (scale bar = 5 mm), and t, penis (scale bar = 5 mm), of holotype, NMV F65666, 29.4 mm ML. *Megaleledone senoi* Taki: u, oral, and v, lateral, detail of hectocotylus (scale bar = 10 mm), w, funnel organ (scale bar = 20 mm), and x, penis (scale bar = 20 mm), of NMV F60488, 207.0 mm ML.

Table 1. Taxonomic status of nominal species of *Pareledone* and *Megaleledone* from the Southern Ocean

Species	Status
Pareledone adelieana (Berry, 1917)	Valid (previously designated a *nomen dubium* by Voss, 1988)
Pareledone antarctica (Thiele, 1920)	Probable junior synonym of *Pareledone turqueti* (Joubin, 1905)
Pareledone aurorae (Berry, 1917)	Junior synonym of *Pareledone charcoti* (Joubin, 1905)
Pareledone charcoti (Joubin, 1905)	Valid
Pareledone framensis (this paper)	Valid
Pareledone harrissoni (Berry, 1917)	Valid (previously designated a *nomen dubium* by Voss, 1988)
Pareledone polymorpha (Robson, 1930)	Valid
Pareledone prydzensis (this paper)	Valid
Pareledone turqueti (Joubin, 1905)	Valid
Pareledone umitakae Taki, 1961	Junior synonym of *Pareledone adelieana* (Berry, 1917)
Megaleledone senoi Taki, 1961	Valid

Table 2. Comparison of species of *Pareledone* and *Megaleledone* from Prydz Bay vicinity, Antarctica.

Species	*P. adelieana*	*P. charcoti*	*P. framensis*	*P. harrissoni*	*P. prydzensis*	*M. senoi*
Size at Maturity: male	>40 mm ML	>35 mm ML	>50 mm ML	>50 mm ML	>25 mm ML	>200mm ML
female	>45 mm ML	>55 mm ML	?	>90 mm ML	?	>230mm ML
Arm Formula	4.3.2.1	4.3.2.1	4.3.2.1	4.3.2.1	4=3=2.1	4=3=2.1
Arm Length (% of TL)	65–69	60–70	73–77	65–78	66–70	66–72
Hectocotylised Arm Sucker Count (HASC)	22–28	31–38	44–51	36–50	26–29	38–40
Opposite Arm Sucker Count (OASC)	26–46	37–54	61–80	37–79	29–36	40–69
Ligula Length Index (LLI)	9.7–15.0	5.0–8.1	5.9–7.5	4.7–10.1	6.5–8.2	~3.6
Head Width (% of MW)	88–118	63–72	56–67	68–84	81–83	60–63
Gill Lamellae Count	6–7	7–8	7–8	8–9	6–7	10–11
Egg Length (mm)	8–9*	11–14*	?	12–15*	?	18–19*

*Mature ovarian eggs

Table 3. Comparison of species of *Pareledone* and *Megaleledone* from Prydz Bay vicinity, Antarctica.

Species	*P. adelieana*	*P. charcoti*	*P. framensis*	*P. prydzensis*	*P. turqueti*	*M. senoi*
Sculpture	Minor papillation; two longitudinal ridges on posterior mantle; traces of ventrolateral ridge	Finely papillate on dorsum; smoother ventrally; ventrolateral ridge	Coarsely papillate all over; diamond pattern of primary papillae on mantle; very large ocular papillae; no ventrolateral ridge	Finely papillate on dorsum; smoother ventrally; traces of ventrolateral ridge	Minor papillation; loose and wrinkled skin; no ventrolateral ridge	Minor papillation; loose and wrinkled skin; fleshy ventrolateral ridge
Colour	Purplish-red dorsally; paler ventrally	Purplish-brown dorsally; paler ventrally	Golden yellow dorsally; paler ventrally; large white spots and stripes on mantle	Purplish-pink mantle dorsum; dark purplish-brown to black brachial crown, web and arms; paler ventrally	Brownish-pink dorsally; paler ventrally	Dark purplish-pink dorsally; paler ventrally
Other Remarks	Mantle elongate ovoid; head wider than mantle; eyes very large; arms short and stout	Mantle roundly ovoid; head narrower than mantle; arms short and tapering	Mantle roundly ovoid; head narrower than mantle; arms long and tapering	Mantle roundly ovoid; head narrower than mantle; arms short and stout; web very deep	Mantle roundly ovoid; head narrower than mantle; arms long and tapering; skin loose and sometimes slightly gelatinous	Mantle roundly ovoid; head narrower than mantle; arms moderately long and stout; web very deep; skin loose and gelatinous

by the collection of females with egg broods, and live rearing experiments. The species have not been recorded from regions other than the Antarctic continental shelf, and may be classified as endemic elements of the fauna.

Acknowledgments

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